An analysis of a stochastic process of the logistic form.

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AN ANALYSIS OF A STOCHASTIC PROCESS OF THE LOGISTIC FORM

Submitted by R.H. NORDEN for the degree of Ph.D. of the University of Bath.

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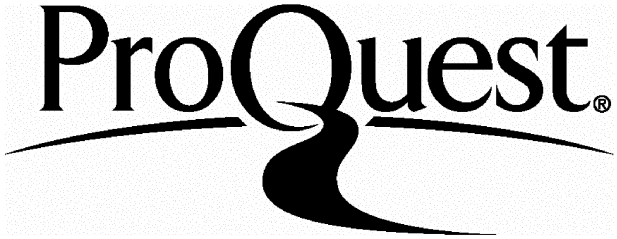

SUMMARY

This thesis is concerned initially with a stochastic logistic, (SL), analogue of VERHULST's equation to describe the growth of an isolated population in a limited environment. An essential feature of the SL process is that extinction will occur with probability 1, and so to begin with the analysis is concerned with the distribution of extinction times in terms of the basic parameters, which are the birth and death rates and the upper limit, N, to the integer state variable, j.

The analysis then continues with an investigation into the form of the distribution of j at time t, and for small t an approximate analytic result for the related PGF is obtatined. For larger t a LAPLACE Transform solution, inverted numerically, is found to be an effective method of evaluating the moments of this distributon, and this may be extended to very large t , if necessary, by considering the process conditional on non - extinction.

A diffusion approximation to the SL process is then derived, and this not only extends the numerical methodology developed so far to the large N situation, but also provides a simple overall view of the SL process itself.

The model is then modified so as to incorporate age and/or time dependent birth and death parameters, and theoretically it is shown that extinction will occur with probability 1 for a large class of such processes. The way in which the distribution of extinction times, in particular, and the overall behaviour of the process, in general, depend on the additional parameters is then investigated by

simulation, and in this respect it is found useful to consider also the corresponding deterministic processes for which numerical solutions can be found.

Finally the model is developed futher so as to describe the sheep populations of the islands of St. Kilda.

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CONTENTS

CHAPTER 1

INTRODUCTION

1.1 THE DETERMINISTIC LOGISTIC EQUATION

The logistic equation which was first proposed by VERHULST (1838) as a way of describing population growth has been the subject of much theoretical and experimental investigation. Subsequently many developements and modifications of this model have been considered, so that a further investigation demands at the outset a clarification as to what form of the model is to be considered, and what justification, especially in biological terms, there is for the form of parametrisation adopted.

Historically there have been two different approaches to the construction of the model. The first was to regard the equation

$$\dot{n} = an - bn^2 \quad (a,b > 0) \ (*) \qquad (1)$$

as an intuitively reasonable way of of describing population growth in a limited environment. The inhibiting effect of the quadratic term on the right hand side of equation (1) implies an equilibrium level $n_E = a/b$ to which the process level tends as $t \to \infty$. If, as is usual, $n(0) < n_E$, then clearly $n(t) < n_E$ for all t, and thus in terms of the model n_E is also the implied carrying capacity of the population's

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(*) In this notation, n(t) is the population size at time t given an initial level n(0). As usual, $\dot{n}$ means $\frac{dn}{dt}$, where $n \equiv n(t)$. Of course, n(t) must necessarily be an integer, whereas equation (1) regards it as a continuous variable. This is not a matter of any consequence.

environment. All this is clearly evident from the solution

$$n(t) = \frac{an(0)}{bn(0) + [a - bn(0)]e^{-at}} \qquad (2)$$

which may easily be obtained by elementary methods.

Otherwise in this approach, no specific biological meaning is attached initially to the parameters a and b. This is essentially the conceptual approach of VERHULST himself in his foundation paper, and later of PEARL and REED (1920) in their well known paper on the growth of the population of the USA.

The alternative approach is that of VOLTERRA (1928) and GAUSE (1934) who did specify the constants a priori in biological terms. In this way they opened up the experimental approach to the direct verification of the model. Nevertheless, whatever approach is adopted the primary motivation for the construction of this model is the aim to describe density dependent population growth in very broad terms.

The question as to what extent animal populations are controlled by density dependent factors , such as availability of food and intra-specific competition, or by density independent factors such as climate, has much exercised biologists and field workers generally, especially during the last two decades. An extensive survey of the various attempts that have been made to resolve this problem will be found, for example, in MCLAREN (1971). Nevertheless, despite the vast amount of field work and experimentation that has been carried out, especially with Microtus, to testa wide range of hypotheses, there are still no generally established principles for animal population regulatory mechanisms.

On the other hand, there are certainly some instances where density dependence is the main factor inhibiting population growth,(*) e.g. CREW and MIRSKAIA (1931), KALELA (1957), HOFFMAN (1958), KOSHKINA (1965 and 1966) and GILL (1972), and to which the logistic model might well be applicable. Beyond this there have been a number of explicit successful attempts to verify the model of which the classic paper of PEARL and READ, to which reference has just been made, is perhaps the most well known. Beyond this we have e.g., ERRINGTON (1951), FUJITA and UTIDA (1953) and SMITH (1963). Also, reviews of attempts by some earlier experimenters to fit the logistic model to laboratory and field data will be found in PRATT (1943) and ALLEE et al. (1949).

There have been instances, however, where attempts to validate the model have failed, e.g., RABINOVICH (1969), so that despite its wide applicability it cannot be regarded, at least in its original deterministic form, as providing a general law to which all density dependent population growth must conform.

The question of what parametrisation to adopt in the logistic model has been considered in some detail by several biomathematicians. A full account of this problem may be found for example in JENSEN (1975). It is not intended to summarise that discussion here, but it will be sufficient to remark at this stage that for most biological populations whose growth may be described by the logistic equation,

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(*) Statistical techniques have been developed to determine whether on the basis of given population data, density dependent factors may be inferred to be operating. See, for example, BULMER (1975) and MINER (1932).

it is unsatisfactory to work with only two independent parameters, as in the case of the fundamental equation (1). At the very least, it will usually be necessary to incorporate three parameters into the model so that apart from the carrying capacity N, the birth and death rates may be specified separately. Thus in place of (1) a more realistic equation is

$$\dot{n} = \lambda n(1 - \frac{n}{N}) - \mu n \qquad (3)$$

where now λ is the birth rate per individual that would be realised in the absence of density dependent checks, and μ is the corresponding death rate. As the stochastic (MARKOV) analogue of (3) forms the subject matter of the early part of this thesis, then equation (3) will be referred to as the L model and its stochastic counterpart as the SL model, even though these definitions are unlikely to gain general acceptance.

Further developments are, of course, posssible. Thus PIELOU (1969) proposes that the birth and death rates per individual be specified as $a_1 - b_1 n$ and $a_2 + b_2 n$ respectively, with a_1, b_1, a_2 and b_2 all positive. This would be a more satisfactory formulation for situations where the death rate increased with population density. This more general model is not considered here, however, partly because the introduction of a fourth parameter would complicate results, and partly because there are certainly situations e.g. CLOUGH (1965) where the birth rate, but not the death rate, is density dependent. Nevertheless it should be emphasised that the techniques developed in this research for the SL process could equally well be applied to the stochastic version of the PIELOU model, and to many other similar models as well.

Finally in conclusion to this section it should be remarked that the literature referred to so far deals only with deterministic versions of the logistic model. The fundamental question as to what extent any conclusions drawn from such models might have to be modified when a stochastic version is used instead is not considered in any of that work. Nevertheless, this question motivates one of the main aims of this thesis.

1.2 STOCHASTIC ANALOGUES OF DETERMINISTIC MODELS

The view that stochastic models are better suited to describe the development of biological populations, rather than their deterministic counterparts, has been gaining support, e.g., LEVINS (1969), LEWONTIN and COHEN (1969), LADDE and SILJAK (1975) and PRAJNESHU (1976). Undoubtedly there is an increasing awareness of the limitations of deterministic models. The concept that it is possible to predict precisely the poulation level at time t given certain initial conditions and rates of change, as is the case, for example, in mechanical systems, seems unreal.

Although not within the scope of this thesis, one must remark in passing that much of the theoretical work on predator - prey models and species interaction problems, in general, e.g. DUTT et al. (1975) and CUSHING (1976), now stands in need of substantial revision in the light of corresponding probabilistic investigations, e.g. BARTLETT (1957), LESLIE and GOWER (1958), MOUNTFORD (1971) and GETZ (1976). Also MOLLISON (1977) in an important survey paper on spatial contact

models gives instances of nonlinear epidemic situations of which the deterministic and stochastic models give fundamentally different accounts. Clearly, these examples in themselves are sufficient to motivate an enquiry into possible essential differences between the L and SL models defined previously. In fact, such a difference will be shown to exist in that in contrast to the equilibium level $n_E = N(1 - \mu/\lambda)$, $(\lambda > \mu)$, to which $n(t)$ of the L model tends as t tends to infinity, the mean of the distribution of states, π_t, of the SL description tends to 0 as t tends to infinity. Moreover, extinction is certain. Thus unlike in the simple birth and death process, which may be regarded as the limiting form of the SL process as $N \to \infty$, the deterministic solution is not equal to the mean of the stochastic solution.

One obvious limitation of the deterministic model 1.1(1) is that there is no proper distinction between carrying capacity and the equilibrium level. This has caused some confusion in the literature. That it is essential to make this distinction is abundantly clear from the results of both field and laboratory studies. Thus CALHOUN (1952), KING (1955) and CHRISTIAN (1971), and many others, record instances where population equilibria, or even maxima, are well below the levels that would be expected in terms of the known levels of environmental factors, such as availability of food, climate, shelter and also predator activity, if any.

It is not the aim of this analysis to investigate the nature of the population regulatory mechanisms which must be operating in such cases. This is essentially a biological question, and there is in any case an extensive literature on this subject already, McLAREN (1971). What is being argued here, however, is that in view of the available biological and ecological data on population dynamics it follows that a model

which does not make clear the difference between the essentially different concepts of carrying capacity and equilibrium level, can have only very limited usefulness. This point will be amplified further in Chapter 6.

In the SL model it is possible for the population to reach the level N, though with small probability, for any $n(0) > 0$. Thus the model implies that the carrying capacity is the maximum population level attainable under any possible set of circumstances that could arise in the actual environment. From the ecological standpoint this seems a reasonable definition.

In general, unless $n(0)$ is very near to 0, in which case it would be likely that extinction would occur almost at once, it would be expected that the population level would remain close to n_E for a long period of time if N is large and/or λ is significantly greater than μ. There would be occasional and random excursions up towards N, and down towards the zero state, and eventually extinction would occur. Clearly this provides greater realism, especially when dealing with small populations, than the large t steady state situation described by the classical deterministic logistic model.

1.3 THEORETICAL DEVELOPMENT

The SL model considered in the early part of this thesis relates to the integer state variable $X(t)$, $(0, 1, 2, \ldots, N)$, which has a probability structure defined by the MARKOV scheme such that for $j = 0, 1, \ldots, N$

$$\left.\begin{aligned} & P\left[X(t+\delta t) = j+k \mid X(t) = j\right] \\ & = \lambda_j \delta t + o(\delta t) \text{ if } k = 1, \\ & = \mu_j \delta t + o(\delta t) \text{ if } k = -1, \\ & = 1 - (\lambda_j + \mu_j)\delta t + o(\delta t) \text{ if } k = 0, \\ & = o(\delta t), \text{ otherwise,} \end{aligned}\right\} \quad (1)$$

where $\lambda_j = \lambda j(1 - \frac{j}{N})$ and $\mu_j = \mu j$.

Anyone therefore approaching the problem of obtaining the probability distribution, π_t, of X(t) for this process in terms of λ, μ and N and the initial state i, would naturally consider first the usual PGF technique as described by KENDALL (1949).(*) As is shown in Chapter 2, however, this leads to an apparently intractable second order partial differential equation for the PGF, G(z,t). It does not appear to come within the fairly wide class of partial differential equations relating to birth and death stochastic (MARKOV) processes for which a useful explicit solution can be obtained, ARLEY (1967). However, various approximation methods have been attempted for stochastic processes of the logistic type, and some results are also available for limiting (stationary) distributions where such exist and take a non - trivial form.

In the first place KENDALL (1949) considers a version of the process where the birth and death rates are now

$$\lambda_j = \alpha j(N_2 - j) \text{ and } \mu_j = \beta j(j - N_1) \quad (2)$$

respectively, and where $N_2 > N_1$ and $\alpha, \beta \geq 0$.

(*) According to BARTLETT (1949) this method was first used by PALM (1943), but was later discovered independently by othe writers. See also footnote on page 299 of ARLEY and BORCHSENIUS (1945).

This is a four parameter system. In particular, if $\beta = 0$, one has a logistic version of the process of FURRY (1937), that is, of what is essentially a pure birth process for which FELLER (1939) has given a complete solution. Clearly, however, such a model cannot be used to describe the growth of biological populations.

Nevertheless, in the general form of his process, where α and β are both strictly positive, KENDALL shows that even though the partial differential equation defining $G(z,t)$ appears intractable, the distribution of states for large t, assumed to exist and to be stationary, may readily be derived. In the ecological context, it would usually be required that $N_1 = 0$, so allowing for the possibility of extinction. A non - zero N_1 could only relate to special environmental circumstances, and would have little generality. However, if in KENDALL'S result for the stationary, large t, distribution, N_1 is allowed to tend to zero, as a continuous variable, then the limiting distribution, $P_0 = 1$ and $P_j = 0$ for $1 \leqslant j \leqslant N$ will be obtained. In other words, extinction is certain. This intuitively reasonable result which may be regarded as a consequence of the theory of MARKOV chains, BARTLETT (1949), is also proved in Chapter 5 of this thesis, but for a much wider class of processes, both Markovian and non - Markovian.

Also KENDALL considered the special case where $N_2 \to \infty$ and $\alpha \to 0$ in such a way that $\alpha N_2 \to \lambda_0$, a positive constant, and showed that, with $N_1 = 1$, then in this case, the limiting distribution is 'modified Poisson'. However, this process is essentially different from the SL process, not only because there is no limit to the population size, but also because the death rate, but not the birth rate, per individual varies with j. Furthermore, as it does not include the zero state it

cannot be applied to any population for which extinction is a possibility.

There is, however, a special case of quadratic birth and death rates which does have some relevance to the type of population growth problem considered here. The background situation is in genetics, and is equivalent to taking

$$\lambda_j = aj(N - j) + bj \text{ and } \mu_j = aj(N - j) + c(N - j) \qquad (3)$$

where $j = 0, 1, \ldots, N$ and $a, b, c > 0$. In this special case, BATHER (1963) found that a complete solution of the partial differential equation defining the MGF, $M(\theta,t)$, appertaining to π_t could be found in terms of standard functions. In fact, it can be shown that his method can be applied to situations where λ_j and μ_j take the form

$$\lambda_j = a'j - b'j^2 \text{ and } \mu_j = c'j - b'j^2 \qquad (4)$$

provided a', b' and c' are all positive, and $c' > a'$. This last condition, however, which implies $\mu_j > \lambda_j$ for all $j \geq 1$ restricts the application of the model to ecological situations of little interest. Also the specification of μ_j/j as a decreasing function of j further restricts the usefulness of the model.

A further development is the perturbation method of BAILEY (1968). The background problem here is in the field of epidemiology, and the 'birth rate', i.e. the rate of increase of infectives takes the form $\lambda_j = \beta j(N - j)$ while $\mu_j \equiv 0$. The resulting partial differential equation for $M(\theta,t)$ is thus second order. Essentially the method consists of regarding $M(\theta,t)$ as differing by a small amount from $M_0(\theta,t)$ the MGF of the corresponding deterministic process which, of course, may readily be determined. In fact, the difference is shown to be $O(N^{-1})$ uniformly with respect to t, and $M(\theta,t)$ is then obtained explicitly within $O(N^{-2})$

Approximate results for the moments of the distribution π_t can then be obtained to the same accuracy.

This method is applied here in Chapter 3, but in view of the large t divergence between the deterministic solution and the stochastic mean, which does not arise in the epidemiological situation considered by BAILEY, the results are valid only for relatively small values of t. However, they do show, at least, that some progress towards a complete explicit solution, capable of rapid numerical evaluation, is possible.

There are, also, a number of other attempts to obtain approximate results for the MGF (or PGF) of π_t for processes of the stochastic logistic form, and which take as a starting point BARTLETT'S (1949) master equation

$$\frac{\partial M}{\partial t} = L\left[\theta, \frac{\partial}{\partial \theta}, t\right] M \qquad (5)$$

In this equation which may be applied to a very large class of birth - death processes, the operator L is linear in $\frac{\partial}{\partial \theta}$, and both its order and form depend, of course, on the parameters of the model.

WHITTLE (1952) shows how, from the purely formal solution of (5) in terms of L, approximate results for the moments of π_t may be obtained. In processes of the logistic type, such results would not, in general, be valid for large t. Also DANIELS (1960 and 1971) developes equation (5) to obtain approximate results for the logistic process, but again these are only valid for small t. In general, such operator methods cannot be applied to obtain valid large t results for processes, such as the SL model, where the deterministic solution differs significantly from the stochastic mean as $t \to \infty$.

There appears therefore to be no explicit results for $M(\theta,t)$, or $G(z,t)$, valid for all t, affording a simple interpretation of the process in theoretical terms and providing a means whereby numerical results may readily be obtained. In any case it is doubtful, in view of the form of equation 2.1(9), whether such results can exist.

In this research, however, considerable emphasis is placed on obtaining numerical results economically in terms of computer time. Various techniques are thus developed to that end. In the later chapters where the model is developed further to achieve greater realism the analysis depends largely on numerical techniques. Nevertheless a number of theoretical results have been established in this research, and it would now seem appropriate to summarise briefly what, in fact, has been achieved both on the theoretical and on the numerical side.

1.4 SURVEY OF ANALYSIS

As remarked previously the certainty of extinction which is a basic feature of the SL process is proved in Chapter 5 for a very wide class of similar processes, where also age and time dependent parameters are admitted. In Chapter 2, however, the general form of π_t for the SL process is determined. Each $p_{ij}(t)$, the probability that the process is in state j at time t, given that it was initially in state i, is shown by LAPLACE transform methods to be a linear combination of negative exponential functions of t. In particular, it is immediately evident from these results that $p_{ij}(t) \to 0$ as $t \to \infty$ if $j \neq 0$, but $p_{i0}(t) \to 1$ as $t \to \infty$.

Formulae are then derived for the moments of T_i, the time to extinction from an initial state i, and the numerical determination of $f_i(t)$, the PDF of T_i, is then possible. Thus T_i is shown to be, very nearly, a Gamma variate. In particular, the consistency of theoretical and simulated results is demonstrated. Finally in Chapter 2 the process conditional on non - extinction is considered, and is shown to be an effective way of determining the large t values of the moments, especially in cases where N is large.

In Chapter 3, π_t is considerd in further detail, though here the discussion is still limited to the SL process. Again the theoretical development is preceded by simulation, from which it is possible to get a good idea of the form of π_t. A first step in the theory is the application of BAILEY'S perturbation method outlined in the previous section. The actual analysis involved, however, is far from simple. The value of the result lies in the fact that it can be very rapidly evaluated over a wide range of parameter values and so provide a check on results obtained in other ways. Also the method could be extended further to obtain approximate results for the MGF up to $O(N^{-3})$, and even beyond.

The numerical evaluation of the process for all t, however, can (*) very effectively be carried out by an application of the numerical inversion technique of BELLMAN et al. (1966) applied to the formal LAPLACE transform solution obtained in Chapter 2. The application of the method in this context does not make heavy demands on computer time. The validity of the method can also be confirmed by considering again the process conditioned on non - extinction, and by the direct numerical integration of the second order differential equation which defines

(*) Except, possibly, for very large t in certain cases.

$G_i(z,t)$, namely equation 2.1(9).

A diffusion approximation to the SL process is considered in Chapter 4. This is motivated by the fact that the formulae for the moments of T_i derived in Chapter 2 are not capable of numerical evaluation when N becomes too large, i.e. greater than about 500. In such cases progress is impeded by the usual computer problems such as overflow, excessive CP time requirements, etc. Nevertheless these difficulties can be resolved by the use of the diffusion approximation. Thus by this stage a complete methodology has been developed whereby the moments of π_t may be determined for all t and all N.

Towards the end of this chapter the theory is developed further. The process conditioned on non - extinction is considered again and its limiting form as $N \to \infty$ is shown to be normal. Also, in this way, it is possible to gain a simple overall view of the process for large N.

The last two chapters are concerned with extensions of the SL process. In chapter 5 time and/or age dependent birth functions are incorporated into the model, though only simple forms are considered. It is in this chapter that the theorem on the certainty of extinction, referred to earlier, is established. Otherwise, the level of complication here precludes any further theoretical advance, and much use has to be made of simulation.

It is in this way, for example, that it is possible to establish the range of critical frequencies in respect of the effect which a cyclic birth function has on the time to extinction, T_i. On the other hand, the investigation of the effect of age - dependent birth and death functions in a numerical way is complicated by the necessity to work

with age groupings of a suitable width. This considerably slows down the simulation of the process, but nevertheless some progress in determining the way in which the age parameters affect T_i was found to be possible. In particular, it was found useful to consider the logistic deterministic process in which the birth function is age but not time dependent. Although a formal solution is not possible, even here, nevertheless numerical results may readily be obtained by LAPLACE transform techniques, together with, again, an application of the numerical inversion procedure of BELLMAN et al. The results so obtained thus form a basis for the appropriate selection of parameter values when considering the stochastic analogue. In addition, it is found that the conclusions established in this way carry over to the process where the birth function is both age and time dependent.

In Chapter 6, a specific ecological example is considered. The SL model is developed to describe the Soay sheep population of HIRTA, ST. KILDA. This is one of the most renowned examples of a relatively small isolated breeding community, and as such is especially suitable for analysis in broad demographic terms by some suitable form of the model. That this is possible is also due to the ' life - table ' data and other relevant information made available by the results of a number of field studies. The birth and death functions are now both age and time dependent. Also the sex and age composition of the population must be taken into account. Thus the model is now a good deal more complicated than in its original SL form, and in this situation the only feasible method of investigation is by simulation.

There is, however, no attempt to achieve an overall energy flow model taking into account all possible biological factors of relevance. Even so a measure of agreement is achieved between simulated and

actual population records. On this basis, therefore, consideration is given to the question of extinction, especially also for the sheep populations of the smaller islands of the ST. Kilda group, and the model indicates that this is certainly a possibility so long as the established birth and death patterns for the colony continue to be maintained.

1.5 MORE GENERAL ECOLOGICAL CONSIDERATIONS

It should be clear now that the aims of this research are not purely theoretical. In particular, there appears to be no reason why the methodology considered here could not usefully be directed to other more complicated ecosystems. In particular, species interaction situations for which the LOTKA - VOLTERRA equations form a prototype model could be considered within a stochastic logistic framework, and again the question of extinction would be the focus of attention. The remarks made in Section 1.2 about deterministic models and their stochastic counterparts leading to different conclusions as well as the results established here would strongly suggest that this would be a very worthwhile area of investigation.

In particular, it is now appropriate to refer to a biological conjecture of SKELLAM (1955). He predicts that for large populations whose growth may be described by the stochastic logistic model, the time to extinction is very large, and in ecological terms is effectively infinite. This is shown to be essentially correct, both in Chapter 2 and Chapter 4, though in the light of the results of Chapter 5 this might stand in need of some qualification in certain cases. Nevertheless, with reference to the work of FISHER et al.(1943)

and WILLIAMS (1953) he remarks that ' .... most of the species present in a locality are represented by very few individuals. In fact, it may well be, because of physiological effects of otherwise inconspicuous genetic change that ecosystems are far more dynamic than they are often made to appear, that the course of ecological events is intrinsically uncertain, and that the earlier naive concept of the balance of nature, if not entirely illusory, is at least when extended to more than a few dominant species a deceptive exaggeration.' Thus the implication is that the results established in this research, indicating that, in general, the mean time to extinction for small communities as described by the model will be small in terms of geological time, may have a much greater range of application than might at first be supposed.

Finally, therefore on the question of extinction it should be remarked that the vast majority of animal species which have ever existed are now extinct, MILLER and BOTKIN (1974). In attempting to explain this course of events investigators usually look for special environmental circumstances of a catastrophic nature. This may not be necessary, however, for it is an obvious consequence of SKELLAM's remarks supported by the results here, that as very long periods of time were involved, extinction could have occured in the absence of any such special factors.

CHAPTER 2

DISTRIBUTION OF EXTINCTION TIMES

2.1 FIRST CONSIDERATIONS

One approach to the problem of obtaining the probability distribution of states at time t, $\{p_{ij}(t)\}$, of the stochastic logistic (SL) process, as defined in Section 1.3, would be to employ the method of KENDALL (1949) by which it is possible to obtain a partial differential equation for $G_i(z,t)$ for the related probability generating function, (PGF).(*)

To apply this here we first establish differential - difference equations for the probabilities $p_{ij}(t)$. They are, in fact, the KOLMOGOROV - CHAPMAN forward equations which can be obtained by considering the process at time 0, t and t + δt. Simple probability arguments therefore lead to the equations

$$p_{ij}(t + \delta t) = (1 - \lambda_j \delta t - \mu_j \delta t)p_{ij}(t) + \lambda_{j-1}p_{i,j-1}(t)\delta t + \mu_{j+1}p_{i,j+1}(t)\delta t + o(\delta t) \qquad (1)$$

for $j = 1,2,\ldots,N-1$, and also

$$p_{i0}(t + \delta t) = p_{i0}(t) + \mu p_{i1}(t)\delta t + o(\delta t) \qquad (2)$$

and $$p_{iN}(t + \delta t) = (1 - \mu_N \delta t)p_{iN}(t) + \lambda_{N-1}p_{i,N-1}(t)\delta t + o(\delta t) \qquad (3)$$

which clearly imply the system of equations

$$p'_{ij}(t) = \lambda_{j-1}p_{i,j-1}(t) - (\lambda_j + \mu_j)p_{ij}(t) + \mu_{j+1}p_{i,j+1}(t) \qquad (4)$$

(*) Note that i defines the initial state and j indexes the states at time t. Hence, in general, $1 \leq i \leq N$ and $0 \leq j \leq N$.

for $j = 1,\ldots,N-1$,

$$p'_{i0}(t) = \mu_1 p_{i1}(t) \tag{5}$$

and

$$p'_{iN}(t) = \lambda_{N-1} p_{i,N-1}(t) - \mu_N p_{iN}(t) \tag{6}$$

where $p'_{ij}(t) \equiv \frac{dp_{ij}(t)}{dt}$, etc.

Alternatively, of course, (4), (5) and (6) can be condensed to the single equation

$$p'_{ij}(t) = \lambda_{j-1} p_{i,j-1}(t) - (\lambda_j + \mu_j) p_{ij}(t) + \mu_{j+1} p_{i,j+1}(t) \tag{7}$$

where, for all i and t, $p_{i,-1}(t) \equiv 0$, $p_{i,N+1}(t) \equiv 0$. (Note that in the SL process $\lambda_0 = \mu_0 = \lambda_N = 0$.)

Multiplying therefore (7) by z^j and summing over j from 0 to N, and noting also that as $G_i(z,t) = \sum_{j=0}^{N} p_{ij}(t) z^j$, then

$$\sum_{j=0}^{N} j p_{ij}(t) z^j = z \frac{\partial}{\partial z} G_i(z,t),$$

and

$$\sum_{j=0}^{N} j^2 p_{ij}(t) z^j = z \frac{\partial}{\partial z} \left[z \frac{\partial}{\partial z} G_i(z,t) \right]$$

etc., one readily obtains

$$\frac{\partial G}{\partial t} = (\lambda z - \mu)(z - 1) \frac{\partial G}{\partial z} - \frac{\lambda}{N}(z - 1) z \frac{\partial}{\partial z}\left(z \frac{\partial G}{\partial z}\right) \tag{8}$$

where $G \equiv G_i(z,t)$, or

$$\frac{\partial G}{\partial t} = (1 - z)(\mu - \lambda_1 z) \frac{\partial G}{\partial z} + \lambda_2 z^2 (1 - z) \frac{\partial^2 G}{\partial z^2} \tag{9}$$

where $\lambda_1 = \lambda(1 - 1/N)$ and $\lambda_2 = \lambda/N$.

Alternatively, using BAILEY'S (1964) ' indicator variable ' technique, let $X_i(t)$ be the state variate at time t for the SL process for which the initial state is i and $M \equiv M_{X_i}(\theta,t)$ the corresponding MGF, $E\left[e^{\theta X_i(t)}\right]$. To simplify the notation now write $X \equiv X_i$, and then

$$M_X(\theta,t+\delta t) = E\left[e^{\theta X(t+\delta t)}\right] = E\left[e^{\theta X(t)+\theta\delta X}\right] + o\left[(\delta t)^2\right].$$

Now $$E\left[e^{\theta X(t)+\theta\delta X}\right] = E\left[e^{\theta X(t)}.E\left\{e^{\theta\delta X}\middle| X(t)\right\}\right] + o\left[(\delta t)^2\right]$$

$$= E\left[\left\{\lambda_X e^{\theta}\delta t + (1 - \lambda_X\delta t - \mu_X\delta t) + \mu_X e^{-\theta}\delta t\right\}.e^{\theta X}\right] + o\left[(\delta t)^2\right],$$

($X \equiv X(t)$). Hence we now have,

$$M_X(\theta,t+\delta t) = M_X(\theta,t) + E\left[\left\{e^{\theta}\lambda_X - (\lambda_X + \mu_X) + e^{-\theta}\mu_X\right\}e^{\theta X}\right]\delta t + o\left[(\delta t)^2\right]$$

which implies that

$$\frac{\partial M_X(\theta,t)}{\partial t} = (e^{\theta} - 1)E\left[\lambda_X e^{\theta X}\right] + (e^{-\theta} - 1)E\left[\mu_X e^{\theta X}\right]$$

$$= \lambda(e^{\theta} - 1)\left[\frac{\partial}{\partial\theta} - \frac{1}{N}\frac{\partial^2}{\partial\theta^2}\right]M_X(\theta,t) + \mu(e^{-\theta} - 1)\frac{\partial M_X(\theta,t)}{\partial\theta}$$

since $\lambda_X = \lambda X(1 - \frac{X}{N})$ and $\mu_X = \mu X$. Thus finally

$$\frac{\partial M_X(\theta,t)}{\partial t} = (\lambda - \mu e^{-\theta})(e^{\theta} - 1)\frac{\partial M_X(\theta,t)}{\partial\theta} - \frac{\lambda}{N}(e^{\theta} - 1)\frac{\partial^2 M_X(\theta,t)}{\partial\theta^2} \quad (10)$$

and the transformation $z = e^{\theta}$ will then show that this is in agreement with equation (9).

Now equation (9), or (10), is a second order partial differential equation of the mixed type for which no solution in terms of standard functions appears to exist. It will not be possible therefore, as in the case of the unrestricted process (i.e. where $N \to \infty$), to obtain $G_i(z,t)$ and hence $F_i(t)$, the distribution function of T_i, the time to extinction from an initial state i, merely by setting $F_i(t) = G_i(0,t)$ (*).

(*) It is an immediate consequence of theorem 2.1 of this chapter that extinction in the SL process will occur with probability 1. This result is also proved in Chapter 5 for a much wider class of processes.

In fact the approach here will be the reverse of that argument. Recall that

$$G_i(1,t) = 1 \quad \text{for all } i \text{ and } t; \quad G_i(z,0) = z^i \qquad (11)$$

so that knowledge of the form of $F_i(t)$, and hence of $G_i(0,t)$, will with equations (11) form a set of boundary conditions sufficient for the numerical integration of (9). This idea is developed further in Section 3.3.

In any case, apart from this, the form of $F_i(t)$ is of interest in its own right, since in ecological terms it relates to the problem of determining the life span of a species within a limited environment.

2.2 THE CERTAINTY OF EXTINCTION

Although theorem 5.1 is sufficient for the purpose of proving that in the case of the SL and many other processes extinction will occur with probability 1, nevertheless it gives very little indication of the inner structure of the SL process. The following theorem, however, does give some insight into the way in which the distribution of states $\{p_{ij}(t)\}$ tends to the limiting form $(1,0,0,\ldots,0)$ as $t \to \infty$. In particular it does show the relevance of LAPLACE transform techniques to an analysis of the SL and similar processes.

Theorem 2.1

The probabilities $p_{ij}(t)$ of the SL process take the form

$$\left.\begin{aligned} p_{ij}(t) &= \sum_{k=1}^{N} \beta_{ijk} e^{-\alpha_k t} \quad \text{for } j = 1,2,\ldots,N, \\ p_{i0}(t) &= 1 + \sum_{k=1}^{N} \beta_{i0k} e^{-\alpha_k t} \end{aligned}\right] \qquad (1)$$

where the α's and β's are t - independent, and also the α's are strictly positive and independent of i.

To prove this the following lemmas will be required.

Lemma 1

If $f_n(x)$, n = 0,1,2,... is a sequence of polynomials such that

$$f_0(x) = 1,\ f_1(x) = x + b_1$$

and $$f_n(x) - (x + a_n)f_{n-1}(x) + b_n f_{n-2}(x) = 0 \quad (n \geq 2)$$

where $a_2, a_3, \ldots$ are real and $b_1, b_2, \ldots$ are real and positive, and if also for each n, $f_n(0) > 0$, then for $n \geq 1$ the roots of $f_n(x) = 0$ are real, distinct and all negative, and for $n \geq 2$ the roots of $f_n(x) = 0$ are separated by those of $f_{n-1}(x) = 0$.

This is almost a standard result and a proof of it may be found, for example, in LEDERMAN and REUTER (1954).

Lemma 2 The eigen values of the matrix

$$Q_N = \begin{bmatrix} -(\lambda_1 + \mu_1) & \mu_2 & \cdots & \cdots & \cdots \\ \lambda_1 & -(\lambda_2 + \mu_2) & \mu_3 & \cdots & \cdots \\ \cdots & \lambda_2 & -(\lambda_3 + \mu_3) & \mu_4 & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & \lambda_{N-2} & -(\lambda_{N-1} + \mu_{N-1}) & \mu_N \\ \cdots & \cdots & \cdots & \lambda_{N-1} & -\mu_N \end{bmatrix}$$

are all real distinct and negative.

Proof.

The characteristic equation of the matrix Q_N is

$$D_N(x) = \det \begin{bmatrix} x+\eta_1 & -\eta_1 & \cdots & & \\ -\xi_2 & x+\xi_2+\eta_2 & -\eta_2 & \cdots & \\ 0 & -\xi_3 & x+\xi_3+\eta_3 & -\eta_3 & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & -\xi_{N-1} & x+\xi_{N-1}+\eta_{N-1} & -\eta_{N-1} & \\ \cdots & & -\xi_N & x+\xi_N+\eta_N & \end{bmatrix} = 0 \quad (2)$$

where $\xi_j = \lambda_{N-j+1}$ and $\eta_j = \mu_{N-j+1}$, $(j = 1,2,\ldots,N)$.

Thus $D_N(x)$ defines a sequence of polynomials such that $D_1(x) = x + \eta_1$ and for $N \geq 2$, we have by expansion by the final row,

$$D_N(x) = (x + \xi_N + \eta_N)D_{N-1}(x) - \xi_N\eta_{N-1}D_{N-2}(x). \quad (3)$$

Also as $D_1(0) = \eta_1$, $D_2(0) = \eta_1\eta_2$, then repeated application of (3) leads to

$$D_N(0) = \eta_1\eta_2\ldots\eta_N > 0.$$

Thus the conditions of Lemma 1 are satisfied by the polynomials $D_N(x)$ and the conclusion follows.

We are now therefore in a position to establish Theorem 2.1.

Proof.

First take LAPLACE transforms of the system of equations 2.1(7) to obtain

$$s\bar{p}_{ij}(s) = \delta_{ij} + \lambda_{j-1}\bar{p}_{i,j-1}(s) - (\lambda_j + \mu_j)\bar{p}_{ij}(s) + \mu_{j+1}\bar{p}_{i,j+1}(s) \quad (4)$$

for $j = 0,1,2,\ldots,N$, where $\bar{p}_{ij}(s) = \int_0^\infty e^{-st}p_{ij}(t)dt$, $(s > 0)$.

Thus $$\underline{A}(s)\underline{\bar{p}}_i(s) = \underline{\ell}_i \qquad (5)$$

where $\underline{A}(s)$ is the matrix

$$\begin{bmatrix} s & -\mu_1 & \cdots & & \\ 0 & s+\lambda_1+\mu_1 & -\mu_2 & \cdots & \\ 0 & -\lambda_1 & s+\lambda_2+\mu_2 & -\mu_3 & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & -\lambda_{N-1} & s+\lambda_{N-1}+\mu_{N-1} & -\mu_N & \\ \cdots & \cdots & -\lambda_{N-1} & s+\mu_N & \end{bmatrix} \qquad (6)$$

and $\underline{\bar{p}}_i(s)$ and $\underline{\ell}_i$ are column vectors of order N + 1 such that

$$\underline{\bar{p}}_i^T(s) = \left(\bar{p}_{i0}(s), \bar{p}_{i1}(s), \ldots, \bar{p}_{iN}(s)\right)$$

and $$\underline{\ell}_i^T = \left(\delta_{0i}, \delta_{1i}, \ldots, \delta_{Ni}\right)$$

Partitioning $\underline{A}(s)$ therefore as

$$\left[\begin{array}{c|ccc} s & -\mu_1 & 0 \cdots & 0 \\ \hline 0 & & & \\ 0 & & \underline{B}(s) & \\ \vdots & & & \\ 0 & & & \end{array}\right] \qquad (7)$$

it is clear that the N × N matrix $\underline{B}(0)$ is the matrix $\underline{Q}_N$ of Lemma2. Thus $\underline{B}(s)$ and hence $\underline{A}(s)$ are non - singular, and so equation (5) can be written as

$$\underline{\bar{p}}_i(s) = \underline{A}(s)^{-1}\underline{\ell}_i \qquad (8)$$

and thus formally, at least, $\underline{\bar{p}}_i(s)$ is uniquely defined.

Note also that $\underline{A}^{-1}(s)$ takes the form

$$\left[\begin{array}{c|ccc} s^{-1} & h_1(s) & h_2(s) & \cdots\cdots\cdots\cdots\ h_N(s) \\ \hline 0 & & & \\ 0 & & \underline{B}^{-1}(s) & \\ \vdots & & & \\ 0 & & & \end{array}\right] \qquad (9)$$

where the $h_i(s)$ are rational functions of s, and so from (8) and (9)

$$\underline{\bar{q}}_i(s) = \underline{B}(s)^{-1}\underline{m}_i \qquad (10)$$

where $\underline{\bar{q}}_i(s)$ and $\underline{m}_i$ are column vectors of order N such that

$$\underline{\bar{q}}_i^T(s) = \left(\bar{p}_{i1}(s), \ldots, \bar{p}_{iN}(s)\right)$$

$$\underline{m}_i^T = \left(\delta_{1i}, \delta_{2i}, \ldots, \delta_{Ni}\right)$$

Now by Lemma 2, $\det[B(s)]$ factorises as

$$(s + \alpha_1)(s + \alpha_2)\ldots(s + \alpha_N)$$

where the α's are positive and distinct. Thus (10) implies that

$$\bar{p}_{ij}(s) = \sum_{k=1}^{N} \frac{\beta_{ijk}}{s + \alpha_k} \quad (j > 0), \qquad (11)$$

where the N^2 numbers β_{ijk} are real, and so transforming (11) back to the t - domain we have

$$p_{ij}(t) = \sum_{k=1}^{N} \beta_{ijk} e^{-\alpha_k t}$$

Finally, since for all t

$$\sum_{j=0}^{N} p_{ij}(t) = 1$$

then $p_{i0}(t)$ must take the form

$$p_{i0}(t) = 1 + \sum_{k=1}^{N} \beta_{0ik} e^{-\alpha_k t}$$

where the β_{0ik} are also real.

An immediate corollary is that the limiting form of the distribution $\{p_{ij}(t)\}$ as $t \to \infty$ is $(1, 0, 0, \ldots, 0)$. A further corollary is that $\mu_i(t)$, the mean of the distribution at time t, takes the form

$$\mu_i(t) = \sum_{k=1}^{N} \gamma_{ik} e^{-\alpha_k t}$$

and that all the higher moments are also linear combinations of negative exponential functions of t.

2.3 SIMULATION

For the rest of this chapter attention will be confined to $f_i(t)$ the density of T_i, the time to extinction in the SL process from an initial state i. As a first step therefore towards getting some idea as to the form of $f_i(t)$, the process was simulated over a range of parameter values, and the results are given in Tables 2.1 and 2.2 at the end of this chapter. Further details with regard to the program, the generation of random numbers etc., will be found in Appendix 1.

The notation SL(λ, μ, i, N) is employed to mean the SL process as defined by equations 1.3(1) with birth and death rates λ and μ respectively, upper limit N and initial state i. In this way a case is defined:

Also $\tau_i = E(T_i)$ and $\sigma_i = V(T_i) = E\left[(T_i - \tau_i)^2\right]$ and $\hat{\tau}_i$ and $\hat{\sigma}_i$, their simulated estimates are, in the case of Table 2.1, based on 50 runs of each case, but because of computer time limitations on only 10 runs of each case in Table 2.2.

With regard to Table 2.1, two aspects of the results stand out clearly. Firstly the very rapid increase in $\hat{\tau}_i$ and $\hat{\sigma}_i$ as the ratio $\phi = \lambda/\mu$ increases. Secondly, the relative values of $\hat{\tau}_i$ and $\hat{\sigma}_i$ in each case suggest that the distribution of T_i is, at least, near to that of a gamma variate. On the other hand, the results of Table 2.2 indicate the way in which τ_i depends on N. As expected, it increases rapidly with N, though on the basis of these results it would be difficult to separate the 'ϕ - effect' from the 'N - effect'. Finally, it is worth pointing out how for $i \geqslant 10$ the effect of i on τ_i decreases as ϕ increases, to become virtually non - existent. Thus for SL(.15, .1, i, 100), for example, τ_i is essentially independent of i for $i \geqslant 10$.

Other cases could also be simulated, but there are enough results here to indicate the main trends. In any case, there are computer time limitations which would certainly be exceeded on any system by runs of e.g. SL(.2, .1, i, 100) or SL(.12, .1, i, 10^7), unless of course i was very close to zero. We therefore pass on to consider the distribution of T_i more from the analytic point of view, bearing in mind, however, the sort of theoretical results it is now reasonable to expect.

2.4 FORMULAE FOR τ_i

It is not difficult to obtain an approximation for τ_i in the case where $\lambda = 0$. Although the result is largely of theoretical interest it does provide a lower bound for τ_i regarded as a function of λ.

In the notation of Section 2.2, if $\lambda = 0$ so that we have a pure death process, then $\theta_j = \mu_j^{-1}$ is the mean sojourn time for each state j, $1 \leqslant j \leqslant N$. Since therefore the process passes through each of the states $i, i-1, i-2, \ldots, 1$ just once, then

$$\tau_i = \mu^{-1} \sum_{j=1}^{i} j^{-1} \tag{1}$$

$$\simeq \mu^{-1} (\gamma + \ell n i) \tag{2}$$

For the general case where $\lambda > 0$ the derivation of formulae for τ_i is a good deal more complicated, and several approaches are possible. We first prove the following.

Theorem 2.2

If in the SL process SL(λ, μ, i, N) the N - vectors $\underline{\tau}$ and $\underline{\theta}$ are such that

$$\underline{\tau}^T = (\tau_1, \tau_2, \ldots, \tau_N) \text{ and } \underline{\theta}^T = (\theta_1, \theta_2, \ldots, \theta_N)$$

where τ_i is the mean time to extinction from an initial state i, and $\theta_j^{-1} = \lambda_j + \mu_j$, and if also

$$\underline{D} = \begin{bmatrix} 0 & \lambda_1' & 0 & \cdots & 0 \\ \mu_2' & 0 & \lambda_2' & \cdots & 0 \\ 0 & \mu_3' & 0 & \lambda_3' & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & \mu_{N-1}' & 0 & \lambda_{N-1}' \\ \cdots & \cdots & 0 & \mu_N' & 0 \end{bmatrix}$$

where $\lambda_j' = \lambda_j/(\lambda_j + \mu_j)$ and $\mu_j' = \mu_j/(\lambda_j + \mu_j)$, then $\underline{I} - \underline{D}$ is a non - singular matrix, where $\underline{I}$ is the $N \times N$ identity matrix, and

$$\underline{\tau} = (\underline{I} - \underline{D})^{-1}\,\underline{\theta}.$$

Proof

In the first place the matrix $\underline{I} - \underline{D}$ which is

$$\begin{bmatrix} 1 & -\lambda_1' & 0 & \cdots \\ -\mu_2' & 1 & -\lambda_2' & \cdots \\ 0 & -\mu_3' & 1 & -\lambda_3' & \cdots \\ \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & -\mu_{N-1}' & 1 & -\lambda_{N-1}' \\ \cdots & \cdots & \cdots & -\mu_N' & 1 \end{bmatrix}$$

is such that all row sums, apart from the first, are zero. Hence its determinant is equal to

$$\det \begin{bmatrix} 1 & -\lambda_1' & \cdots & & \\ 0 & 1 & -\lambda_2' & \cdots & \\ \cdots & \cdots & \cdots & \cdots & \\ \cdots & -\mu_{N-1}' & 1 & -\lambda_{N-1}' & \\ \cdots & & -\mu_N' & 1 & \end{bmatrix}$$

and hence to the $N-1 \times N-1$ determinant

$$\det \begin{bmatrix} 1 & -\lambda_2' & \cdots & & \\ -\mu_3' & 1 & -\lambda_3' & \cdots & \\ \cdots & \cdots & \cdots & \cdots & \\ \cdots & -\mu_{N-1}' & 1 & -\lambda_{N-1}' & \\ \cdots & & -\mu_N' & 1 & \end{bmatrix}$$

and by repetition of this argument it is clear that $|I - D| = 1 \neq 0$.

Now consider the imbedded MARKOV chain M with probability transition matrix,

$$\underline{C} = \begin{bmatrix} 1 & 0 & \cdots & & 0 \\ \mu_1' & 0 & \lambda_1' & 0 & \cdots & 0 \\ 0 & \mu_2' & 0 & \lambda_2' & 0 & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & \cdots & \mu_{N-1}' & 0 & \lambda_{N-1}' & & \\ 0 & \cdots & & \mu_N' & 0 & & \end{bmatrix} \qquad (1)$$

Clearly $\underline{D}$ is a submatrix of $\underline{C}$, though not itself a stochastic matrix.

If now X_k is the state appertaining to M immediately after the k^{th} transition ($k = 0,1,2,\ldots$), then define

$$g_{ij} = P(X_\ell = j \text{ for some } \ell > k \mid X_k = i). \tag{3}$$

Thus g_{ij} is independent of k since M is a MARKOV process. Hence if N_{ij} is the number of times spent by the process in state j in passing from the initial state i to state 0, then for $j \neq i$,

$$P(N_{ij} = 0) = 1 - g_{ij}$$

and $$P(N_{ij} = n) = g_{ij}(1 - g_{jj})g_{jj}^{n-1} \quad \text{for } n \geq 1.$$

Writing therefore $\nu_{ij} = E(N_{ij})$, it follows that

$$\nu_{ij} = g_{ij}(1 - g_{jj}) \sum_{n=1}^{\infty} j g_{jj}^{n-1} = \frac{g_{ij}}{1 - g_{jj}} . \tag{4}$$

Similarly for $j = i$,

$$\nu_{ii} = 1 + \frac{g_{ii}}{1 - g_{ii}} = \frac{1}{1 - g_{ii}} \tag{5}$$

Now define T_{ijk} as the k^{th} sojourn time for state j, and T_{ij} as the total time spent by the process in state j. Then,

$$T_i = \sum_{j=1}^{N} \sum_{k=1}^{N_{ij}} T_{ijk} = \sum_{j=1}^{N} T_{ij} \tag{6}$$

Also $$E(T_{ij}) = \underset{N_{ij}}{E} \left\{ \underset{j}{E}(T_{ij} \mid N_{ij}) \right\} \tag{7}$$

where on the right hand side of (7) the outer expectation is taken with respect to the distribution of N_{ij} and the inner expectation with with to the distribution of sojourn times for state j. Further,

$$E_j(T_{ij} \mid N_{ij}) = E_j\left\{\sum_{k=1}^{N_{ij}} T_{ijk} \mid N_{ij}\right\}$$

$$= \sum_{k=1}^{N_{ij}} E_j(T_{ijk} \mid N_{ij}) = N_{ij}\theta_j \tag{8}$$

so that from (7) and (8)

$$E(T_{ij}) = E_{N_{ij}}(\theta_j N_{ij}) = \theta_j \nu_{ij} \tag{9}$$

Combining (6) and (9) therefore, we have

$$E(T_{i.}) = \sum_{j=1}^{N} E(T_{ij}) = \sum_{j=1}^{N} \theta_j \nu_{ij} \tag{10}$$

which in view of (4) and (5) implies that

$$\tau_i = \theta_i + \sum_{j=1}^{N} \frac{\theta_j g_{ij}}{1 - g_{jj}} \tag{11}$$

Now from the standard theory of MARKOV chains, e.g. COX and MILLER (1965), Chapter 3, it is known that if

$$f_{ij}^{(n)} = P(X_{k+n} = j \text{ and } X_{k+\ell} \neq j \text{ for } 1 \leqslant \ell \leqslant n - 1 \mid X_k = i) \tag{12}$$

and $$p_{ij}^{(n)} = P(X_{k+n} = j \mid X_k = i) \tag{13}$$

both of which are, of course, independent of k, then the generating functions

$$P_{ij}(z) = \sum_{n=1}^{\infty} p_{ij}^{(n)} z^n \tag{14}$$

and $$F_{ij}(z) = \sum_{n=1}^{\infty} f_{ij}^{(n)} z^n \tag{15}$$

are related by

$$F_{ij}(z) = \frac{P_{ij}(z)}{1 + P_{jj}(z)} \tag{16}$$

Thus $$g_{ij} = \sum_{n=1}^{\infty} f_{ij}^{(n)} = \frac{P_{ij}(1)}{1 + P_{jj}(1)} \qquad (17)$$

and so from (11) and (17)

$$\tau_i = \theta_i + \sum_{j=1}^{N} P_{ij}(1)\theta_j . \qquad (18)$$

Putting z = 1 in (14) therefore shows that (18) can be written as

$$\tau_i = \theta_i + \sum_{j=1}^{N} \theta_j \sum_{n=1}^{\infty} p_{ij}^{(n)} \quad (*)$$

$$= \theta_i + \sum_{n=1}^{\infty} \sum_{j=1}^{N} \theta_j p_{ij}^{(n)} \qquad (19)$$

the reordering of summation being justified as the infinite series involved consist only of positive terms and are convergent.

Observing therefore that the (N + 1) × (N + 1) matrix of n - step probabilities $\left\{ p_{ij}^{(n)} \right\}$, (i,j = 0,1,2,...,N), is $\underline{C}^n$, and $\underline{C}^n$ partitions to

$$\underline{C}^n = \left[\begin{array}{c|c} 1 & \underline{0}_n^T \\ \hline \underline{b}_n & \underline{D}^n \end{array}\right]$$

where $\underline{b}_n$ is an n - vector and $\underline{0}_n^T$ is the n - vector (0, 0,...,0), then it is clear that the N χ N matrix $\left[p_{ij}^{(n)} \right]$, (i,j = 1,2,...,N), is $\underline{D}^n$.

Thus taking i = 1,2,...,N the equation

(*) The series $\sum_{n=1}^{\infty} p_{ij}^{(n)}$ is convergent for all $j \geq 1$, since all states j, $1 \leq j \leq N$ are non - recurrent.

$$\underline{\tau} = \underline{\Theta} + \left[\sum_{n=1}^{\infty} \underline{D}^n\right] \underline{\Theta} \quad (*) \qquad (20)$$

is obtained. Since therefore, as we have already proved, $(\underline{I} - \underline{D})$ is non.- singular, then

$$\underline{I} + \sum_{n=1}^{\infty} \underline{D}^n = (\underline{I} - \underline{D})^{-1} \qquad (21)$$

and so the final result

$$\underline{\tau} = (\underline{I} - \underline{D})^{-1}\underline{\Theta} \qquad (22)$$

follows immediately.

This result, which to the best of the author's knowledge is completely new, does therefore give a general formula for the mean time to extinction for all initial states in a compact form. It is also quite general in that it will apply to any similar process for which extinction is certain. Its obvious limitation is that it does not appear to indicate in a simple way the dependence of $\underline{\tau}$ on the basic parameters λ, μ and N, though it is doubtful whether, in any case this can be achieved solely in analytic terms. On the other hand,

---

(*) The series $\sum_{n=1}^{\infty} \underline{D}^n$ is convergent in the usual sense that there exists an $N \times N$ matrix $\underline{D}_0$ such that $\lim_{M\to\infty}\left\{\sum_{n=1}^{M} \underline{D}^n\right\}_{ij} = \underline{D}_{0ij}$ for every $(ij)^{th}$ element, $1 \leqslant i \leqslant N$, $1 \leqslant j \leqslant N$. That it is convergent is clear from the convergence of $\sum_{n=1}^{\infty} p_{ij}^{(n)}$ to ℓ_{ij}, say, so that in fact $\underline{D}_0$ is the $N \times N$ matrix $\{\ell_{ij}\}$.

with the aid of a computer it is a simple matter to evaluate (22), especially if routines for standard matrix operations are available.

A more explicit form for the τ_i can, however, be established by a completely different argument. The result obtained can be shown to be consistent with (22), as of course it must be, but this deduction is certainly not obvious. For this reason the statement and proof of the alternative form for τ_i is embodied in a separate theorem.

Theorem 2.3

For any stochastic birth - death process with birth and death rates λ_j and μ_j respectively, such that extinction is certain, the mean time to extinction τ_i, for an initial state i is given by

$$\tau_i = \sum_{j=1}^{i} \psi_j \sum_{k=j}^{N} (\mu_k \psi_k)^{-1} \qquad (23)$$

where $\psi_k = \phi_k \phi_{k+1} \cdots \phi_{N-1}$ for $1 \leq k \leq N-1$, $\psi_N = 1$ and $\phi_k = \lambda_k/\mu_k$.

Proof

With the notation of the previous theorem, let

$$d_j = 1 - g_{j,j+1} \quad (j = 1,2,\ldots,N-1)$$

so that $1 - d_j$ is the probability that the process goes above state j. Also, standard probability arguments lead to

$$1 - d_j = \lambda_j' + (1 - d_{j-1})(1 - d_j)\mu_j' \quad (*) \qquad (24)$$

and hence

$$e_j = \phi_j e_{j-1} + 1 \qquad (25)$$

where $e_j = d_j^{-1}$. Thus

$$e_j = 1 + \phi_j + \phi_j\phi_{j-1} + \cdots + \phi_j\phi_{j-1} \cdots \phi_1 \qquad (26)$$

(*) The author is indebted to Professor SIBSON for drawing his attention to this method of solution.

Now for $j > i$,

$$g_{ij} = g_{i,i+1}g_{i+1,i+2} \cdots g_{j-1,j} \tag{27}$$

and as also $g_{k,k+1} = 1 - e_k^{-1}$ for $k = 1,2,\ldots,N-1$, then

$$g_{ij} = (1 - e_i^{-1}) \ldots (1 - e_{j-1}^{-1}) \tag{28}$$

For $j = i$, $\quad g_{ii} = \lambda_i' + \mu_i' g_{i-1,i} = \lambda_i' + \mu_i'(1 - e_{i-1}^{-1})$ (29)

and thus $$g_{ii} = 1 - (1 + \phi_i)^{-1} e_{i-1}^{-1}. \tag{30}$$

In addition, since extinction is certain then

$$g_{ij} = 1 \quad \text{for } j < i. \tag{31}$$

Combining therefore (28),(30) and (31) with (11) we now have

$$\tau_i = \sum_{j=i+1}^{N} (1 + \phi_j)e_{j-1}(1 - e_i^{-1}) \ldots (1 - e_{j-1}^{-1})\theta_j$$

$$+ (1 + \phi_i)e_{i-1}\theta_i + \sum_{j=1}^{i-1} (1 + \phi_j)e_{j-1}\theta_j \tag{32}$$

Noting therefore that

$$(1 + \phi_j)\theta_j^{-1} = \mu_j \tag{33}$$

that (26) can be written as

$$e_j = \psi_{j+1}^{-1} \sum_{k=1}^{j+1} \psi_k \tag{34}$$

and by using (25) and (34) that

$$e_{j-1}(1 - e_i^{-1})(1 - e_{i+1}^{-1}) \ldots (1 - e_{j-1}^{-1}) = \psi_j^{-1} \sum_{k=1}^{i} \psi_k \tag{35}$$

then (32) will be seen to reduce to

$$\tau_i = \sum_{j=i+1}^{N} (\mu_j\psi_j)^{-1} \sum_{k=1}^{i} \psi_k + \sum_{j=1}^{i} (\mu_j\psi_j)^{-1} \sum_{k=1}^{j} \psi_k \tag{36}$$

which is equivalent to (23) as required.

To show that (22) and (23) are consistent, first write (22) as

$$-\mu_i'\tau_{i-1} + \tau_i - \lambda_i'\tau_{i+1} = \theta_i \qquad (37)$$

for $i = 1,2,\ldots,N$, and $\tau_{N+1} \equiv 0$, and then substitute for τ_i etc., by using (23). There is a lot of heavy algebra involved, however, and the details are not therefore given here.

It has already been pointed out that the results of theorems 2.2 and 2.3 apply not only to the SL process, but to any stochastic birth - death process for which extinction is certain. In particular, consider the case where $\lambda_j = \lambda j$ and $\mu_j = \mu j$ where $\lambda < \mu$, which is such a process. In this case $\psi_k = \phi^{N-k}$ where $\phi = \lambda/\mu < 1$ and thus letting $N \to \infty$ in (23) we obtain

$$\tau_1 = \mu^{-1} \sum_{j=1}^{\infty} j^{-1}\phi^{j-1} = -\lambda^{-1}\ell n(1 - \phi) \qquad (38)$$

as the mean time to extinction for a population starting with one individual.

On the other hand $F_1(t)$, the distribution function of T_1, is given by

$$F_1(t) = \frac{1 - e^{kt}}{\phi - e^{kt}} \quad (k = \mu - \lambda), \qquad (39)$$

COX and MILLER(1965), Chapter 4, and so

$$\tau_1 = \lim_{X\to\infty} \int_0^X tF_1'(t)dt$$

$$= \lim_{X\to\infty} \left\{ \frac{X(1 - e^{-kX})}{1 - \phi e^{-kX}} - X + \frac{1 - \phi}{k\phi} \ell n \left[\frac{1 - \phi e^{-kX}}{1 - \phi} \right] \right\}$$

$$= -\lambda^{-1}\ell n(1 - \phi)$$

in agreement with (38).

In the case of the SL process, (23) reduces to

$$\tau_i = \mu^{-1}\sum_{j=1}^{i}(N-j)!\omega^j\sum_{k=j}^{N}\frac{1}{k.(N-k)!}.\omega^{-k} \qquad (40)$$

where $\omega = N\phi^{-1} = \mu\lambda^{-1}N$.

However any attempt to obtain an asymptotic expansion of (40) in ascending of powers of N^{-1}, for large N with (38) as the dominant term, would have to be on the basis of $\lambda \leqslant \mu$, for if $\lambda > \mu$ extinction is not certain in the unrestricted process. This is unfortunate, for in reality, only cases where $\lambda > \mu$ are of much interest and under this condition little theoretical development of (40) appears to be possible.

A further limitation on theorems 2.2 and 2.3 is that the methods used in their proof do not appear to generalise to the higher moments. To obtain these the method of GOEL and RICHTER - DYN (1974) will be used and an outline of its derivation will be given in the next section.

2.5 THE HIGHER MOMENTS OF T_i.

In the first place consider the backward equations for $f_i(t)$ the PDF of the time to extinction, T_i, from an initial state i, for $1 \leqslant i \leqslant N-1$. These are,

$$f_i'(t) = \lambda_i f_{i+1}(t) - (\lambda_i + \mu_i)f_i(t) + \mu_i f_{i-1}(t) \qquad (1)$$

Also for $i = N$, we have

$$f_N'(t) = \mu_N f_{N-1}(t) - \mu_N(t) f_N(t) \qquad (2)$$

Further $f_0(t) = \delta(t)$, where $\delta(.)$ is the DIRAC impulse function,

and moreover there are the boundary conditions

$$f_i(0) = 0 \quad \text{for } 1 \leqslant i \leqslant N.$$

Taking LAPLACE transforms of equations (1) and (2), therefore, leads to the system

$$(s + \lambda_i + \mu_i)\overline{f}_i(s) = \lambda_i \overline{f}_{i+1}(s) + \mu_i \overline{f}_{i-1}(s) \tag{3}$$

for $1 \leqslant i \leqslant N - 1$, and

$$(s + \mu_N)\,\overline{f}_N(s) = \mu_N \overline{f}_{N-1}(s) \tag{4}$$

where $\overline{f}_i(s) = \int_0^\infty e^{-st} f_i(t)dt$. Thus $\overline{f}_0(s) = 1$.

Now since $\left.\dfrac{d^j \overline{f}_i(s)}{ds^j}\right|_{s=0} = (-1)^j M_{ij}$

where $M_{ij} = E(T_i^j)$, then differentiating (3) and (4) j times and setting $s = 0$, we obtain

$$(\lambda_i + \mu_i)M_{ij} - \lambda_i M_{i+1,j} - \mu_i M_{i-1,j} = jM_{i,j-1} \tag{5}$$

for $1 \leqslant i \leqslant N - 1$ and

$$\mu_N M_{Nj} - \mu_N M_{N-1,j} = jM_{N,j-1} \tag{6}$$

Also, $M_{00} = 1$ and $M_{0j} = 0$ for $j \geqslant 1$. (7)

The solution of the equations (5) and (6) with the conditions (7) follows along standard lines and the final result is

$$M_{ij} = j\sum_{k=1}^{i} \psi_k \sum_{\ell=k}^{N} (\mu_\ell \psi_\ell)^{-1} M_{\ell,j-1} \tag{8}$$

where, as previously, $\psi_k = \phi_k \phi_{k+1} \cdots \phi_{N-1}$ for $1 \leqslant k \leqslant N - 1$, $\psi_N = 1$ and $\phi_k = \lambda_k/\mu_K$.

Clearly, when $j = 1$, (8) reduces to (23) of the previous section.

2.6 NUMERICAL DETERMINATION OF $f_i(t)$

The evaluation of M_{ij} by means of (8) of the previous section, which is recursive on j, is easily carried out with the aid of a computer and a large number of different cases can be considered in this way. In fact here, moments of up to order 6 were evaluated for $\lambda = 0.08, 0.09, \ldots, 0.15, \mu = 0.1$, $N = 100$ and $i = 10, 20, \ldots, 100$.

However, there is some restriction on the value of N, for on most systems overflow would occur for $N > 150$, and would certainly occur on any system when $N > 500$ for the range of $\phi = \lambda/\mu$ considered here. Nevertheless this problem is partially resolved by the method of Section 2.7 of this chapter.

Since the results of simulation as shown in Tables 2.1 and 2.2 strongly suggest that the density $f_i(t)$ approximates to that of a gamma variate, whatever the value of i, then the PDF

$$h(t) = \frac{(t/b)^{c-1}}{b\Gamma(c)} e^{-t/b}$$

was fitted exactly to the calculated first and second moments M_{i1}, $(= \tau_i)$ and M_{i2} for a range of values of i. This requires that

$$M_{i1} = bc \quad \text{and} \quad M_{i2} = b^2c(c+1)$$

and so $b = M_{i2}/M_{i1} - M_{i1}$ and $c = M_{i1}^2/(M_{i2} - M_{i1}^2)$.

(*) For this very reason the fitting of an EDGEWORTH expansion cannot be expected to produce satisfactory results. As is shown, for example, in KENDALL and STUART (1963), Vol. 1, Chapter 6, the associated EDGEWORTH expansion for a gamma variate has coeffecients whose absolute value decreases irregularly and a large number of terms would have to be taken therefore in order to obtain a good approximation.

A comparison was then made of the 3^{rd}, 4^{th}, 5^{th} and 6^{th} moments of $f_i(t)$ and $h(t)$. Some results are shown in Table 2.3.

It is also interesting to compare the theoretical mean τ_i and standard deviation σ_i with simulated results for $\hat{\tau}_i$ and $\hat{\sigma}_i$. If $\hat{\tau}_i$ and $\hat{\sigma}_i$ are calculated from 50 runs of each case, then it is reasonable to assume normality for the distribution of $\hat{\tau}_i$. On this basis therefore the interval

$$\left(\tau_i - \frac{1.96\sigma_i}{\sqrt{50}}, \tau_i + \frac{1.96\sigma_i}{\sqrt{50}} \right)$$

could be expected, in accordance with the standard elementary theory, to include 95% of the values of $\hat{\tau}_i$ over a large number of cases. In fact, here it was found that it included $\hat{\tau}_i$ in 76 out of the 80 cases SL(λ, .1, i, 100) for λ = 0.08, 0.09, ... , 0.15 and i = 10, 20, ... , 100, hence showing good agreement between theory and simulation. Some further results are shown in Table 2.4.

2.7 THE DISTRIBUTION OF STATES CONDITIONAL ON NON-EXTINCTION

The restriction on the magnitude of N to which reference was made in the previous section places a major limitation on the usefulness of the theory developed so far. For this reason an entirely different approach to the problem of determining $f_i(t)$, at least approximately, will be adopted which consists essentially of considering the distribution $\left\{q_{ij}(t)\right\}$, $1 \leq j \leq N$, of states at time t conditional on extinction not having occurred.(*) In particular, if $\left\{Q_j\right\}$

(*) The author is indebted to Professor SIBSON for suggesting to him this way of considering the problem and for outlining the method of solution that follows.

is the limiting form of $\left\{q_{ij}(t)\right\}$ as $t \to \infty$, then, as we presently show, there is a very simple approximate relationship between Q_1 and $p_{i0}(t)$, $\left(= F_i(t)\right)$.

In the first place, by differentiating the basic relationship

$$q_{ij}(t) = \frac{p_{ij}(t)}{1 - p_{i0}(t)} \tag{1}$$

with respect to t, we have

$$q'_{ij}(t) = \frac{p'_{ij}(t)}{1 - p_{i0}(t)} + \frac{p_{ij}(t)\, p'_{i0}(t)}{\left[1 - p_{i0}(t)\right]^2} \tag{2}$$

Also equation 2.1(5) can be written as

$$\frac{p'_{i0}(t)}{1 - p_{i0}(t)} = \mu q_{i1}(t) \tag{3}$$

so that combining (2) and (3) the equation

$$\frac{p'_{ij}(t)}{1 - p_{i0}(t)} = q'_{ij}(t) - \mu q_{i1}(t) q_{ij}(t) \tag{4}$$

is obtained, and hence 2.1(4) and 2.1(6) can be written in the form

$$q'_{11}(t) - \mu_1 q_{i1}^2(t) = \mu_2 q_{i2}(t) - (\lambda_1 + \mu_1) q_{i1}(t), \tag{5}$$

$$q'_{ij}(t) - \mu_1 q_{i1}(t) q_{ij}(t) = \lambda_{j-1} q_{i,j-1}(t) - (\lambda_j + \mu_j) q_{ij}(t) + \mu_{j+1} q_{i,j+1}(t) \tag{6}$$

for $j = 2, 3, \ldots, N - 1$ and

$$q'_{iN}(t) - \mu_1 q_{i1}(t) q_{i,N}(t) = \lambda_{N-1} q_{i,N-1}(t) - \mu_N q_{i,N}(t) \tag{7}$$

Now the steady state form $\left\{Q_j\right\}$ of $\left\{q_{ij}(t)\right\}$ is obtained by putting $q'_{ij}(t) = 0$ for $j = 1, 2, \ldots, N$, and we thus have the following system of equations,

$$-\mu_1 Q_1^2 = \mu_2 Q_2 - (\lambda_1 + \mu_1)Q_1 \tag{8}$$

$$-\mu_1 Q_1 Q_j = \lambda_{j-1} Q_{j-1} - (\lambda_j + \mu_j)Q_j + \mu_{j+1} Q_{j+1} \quad \text{for } j = 2,\ldots,N-1 \tag{9}$$

and
$$-\mu_1 Q_1 Q_N = \lambda_{N-1} Q_{N-1} - \mu_N Q_N \tag{10}$$

These equations define a unique distribution $\{Q_j\}$. It is not, however, possible to obtain an explicit analytic form for the Q's, but with the aid of a computer their numerical evaluation presents no special problems. Further details are given in Appendix 9.

Finally from (3) we now have that for sufficiently large t, $p'_{i0}(t)$ is well approximated by

$$p'_{i0}(t) = \mu Q_1 \left[1 - p_{i0}(t)\right] \tag{11}$$

and hence
$$p_{i0}(t) = 1 - e^{-\mu Q_1 t} \tag{12}$$

and
$$f_i(t) = p'_{i0}(t) = \mu Q_1 e^{-\mu Q_1 t}. \tag{13}$$

Thus for cases where τ_i is sufficiently large a good approximation for it will be τ defined by

$$\tau = (\mu Q_1)^{-1} \tag{14}$$

and this is also an approximation for σ_i. Since therefore Q_1 can easily be evaluated, then in this way numerical approximations for τ_i and σ_i can readily be made available.

Clearly, however, there are some limitations on their validity, quite apart from the basic requirement that τ_i must be large. Firstly the result (14) is independent of i, and secondly the implication of (12) is that T_i is a gamma variate with parameter 1. Neither of these conclusions are true as a cursory examination of Tables 2.3 and 2.4 will readily show. Nevertheless the approximation τ becomes more reliable as ϕ ($= \lambda/\mu$) increases beyond 1. This is to be expected

for the form (12) for the distribution function of T_i is exact if the initial distribution is $\{Q_i\}$ and clearly the probability of effectively reaching this situation is increased as λ is increased, and the probability of early extinction correspondingly reduced.

In Table 2.5 the value of the mean μ_Q, the standard deviation σ_Q and Q_1 for the distribution $\{Q_j\}$, and also τ, for the cases SL(λ, .1, i, 100), where λ = 0.15, 0.16,..., 0.2 are shown. In particular, note the excellent agreement between τ in this table and the values of τ_i in Table 2.4 for the case SL(.15, .1, i, 100) where $i \geq 10$. Beyond this, i.e. with $\phi > 0.15$, the approximation would improve further so that it would certainly be appropriate to use it in any situation for which $\phi \geq 1.5$ and $i/N \geq 0.2$. Moreover, there is no restriction on the magnitude of N as such.

This means therefore that there is a method of determining the value of τ_i precisely for those cases for which in numerical terms the previous theory could not be used. The two methods are, in fact, entirely complementary.

Finally extending the use of this method of approximation further, results for larger N ($\geq$ 100) are given in Table 2.6. The cases considered are SL(λ, .1, i, N) for λ = 0.15, ... , 0.20 and N = 100, 200, ... ,500.

Clearly such numerical results that have been established here and in this chapter generally may have important ecological implications. Nevertheless, it is appropriate to defer this question to the final chapter where the model is extended considerably in order to describe realistically an actual ecologocal situation.

TABLE 2.1

Simulated results for $\hat{\tau}_i$ and $\hat{\sigma}_i$ for SL(λ, .1, i, 100)

i \ λ =	.08	.09	.10	.11	.12	.13	.14	.15
10	71.9	101	123	183	314	757	3020	25300
	42.0	78.5	98.1	132	239	846	2950	20500
20	93.1	122	146	246	437	1390	4100	28100
	47.0	76.3	84.6	182	303	1420	4470	25700
30	102	122	145	223	551	1150	3270	18900
	42.9	59.7	76.3	123	475	1100	2670	16900
40	106	139	179	282	387	1590	4220	23000
	59.0	73.4	93.7	172	268	1170	3940	24500
50	112	118	170	283	515	1050	5020	27500
	40.9	53.8	98.5	201	379	931	3480	28300
60	116	135	159	292	550	1180	4680	20800
	41.1	49.2	76.2	189	514	937	5330	21800
70	112	148	163	253	397	951	4350	25600
	42.4	59.1	79.1	122	299	710	4380	21100
80	115	141	192	219	479	1490	4360	21500
	44.1	53.6	92.2	150	392	1170	3340	23000
90	113	147	185	272	588	1175	4450	25700
	48.9	72.7	92.4	175	293	820	4930	24600
100	108	155	180	269	523	1160	5290	17200
	45.4	67.9	102	162	387	921	4590	16000

In each rectangle first entry is $\hat{\tau}_i$ and second $\hat{\sigma}_i$.

TABLE 2.2 Simulated results for $\hat{\tau}_i$ and $\hat{\sigma}_i$ for SL(λ, .1, i, N)

i	N (λ = .1) 100	N (λ = .1) 1000	N (λ = .1) 10000	N (λ = .11) 100	N (λ = .11) 1000	N (λ = .11) 10000 *
$\frac{N}{10}$	113	560	2.14×10^3	183	1.05×10^4	
	89	270	1.11×10^3	132	9.63×10^3	
$\frac{2N}{10}$	118	609	1.86×10^3	246	1.43×10^4	
	63	341	7.92×10^2	182	1.05×10^4	
$\frac{3N}{10}$	182	539	2.45×10^3	223	6.15×10^3	
	118	218	1.10×10^3	123	2.10×10^3	
$\frac{4N}{10}$	159	525	2.24×10^3	282	1.34×10^4	
	86	219	1.38×10^3	172	9.33×10^3	
$\frac{5N}{10}$	152	482	1.74×10^3	283	7.13×10^3	
	72	191	4.70×10^2	201	5.02×10^3	
$\frac{6N}{10}$	182	457	1.82×10^3	292	8.27×10^3	
	86	193	8.11×10^3	189	4.13×10^3	
$\frac{7N}{10}$	183	547	2.11×10^3	253	1.03×10^4	
	90	254	1.07×10^3	122	8.79×10^3	
$\frac{8N}{10}$	147	564	1.77×10^3	219	5.17×10^3	
	63	153	7.53×10^2	150	2.55×10^3	
$\frac{9N}{10}$	190	718	1.64×10^3	272	8.21×10^3	
	129	272	6.17×10^2	175	7.10×10^3	
N	196	506	2.06×10^3	269	1.01×10^4	
	164	203	6.01×10^2	162	1.01×10^4	

* Insufficient computer time available to simulate these cases to extinction.

TABLE 2.3 Compares moments of order k ($1 \leq k \leq 6$) of $f_i(t)$ with those of fitted distribution $h(t) = \frac{(t/b)^{c-1}}{b\Gamma(c)} e^{-t/b}$

	k = 1	2	3	4	5	6	b	c
SL(.12,.1,10,100)	3.70×10^{2}	2.73×10^{5}	3.05×10^{8}	4.54×10^{11}	8.47×10^{14}	1.89×10^{18}	3.68×10^{2}	1.00
	3.70×10^{2}	2.73×10^{5}	3.02×10^{8}	4.45×10^{11}	8.20×10^{14}	1.81×10^{18}		
	0	0	-9.61×10^{-3}	-2.07×10^{-2}	-3.19×10^{-2}	-4.33×10^{-2}		
SL(.12,.1,50,100)	4.77×10^{2}	3.68×10^{5}	4.14×10^{8}	6.17×10^{11}	1.15×10^{15}	2.57×10^{18}	2.95×10^{2}	1.61
	4.77×10^{2}	3.68×10^{5}	3.93×10^{8}	5.36×10^{11}	8.90×10^{14}	1.74×10^{18}		
	0	0	-4.95×10^{-2}	-1.31×10^{-1}	-2.27×10^{-1}	-3.25×10^{-1}		
SL(.15,.1,10,100)	2.28×10^{4}	1.082×10^{9}	7.70×10^{13}	7.30×10^{18}	8.66×10^{23}	1.23×10^{29}	2.46×10^{4}	.927
	2.28×10^{4}	1.08×10^{9}	7.80×10^{13}	7.53×10^{18}	9.13×10^{23}	1.33×10^{29}		
	0	0	1.37×10^{-2}	3.15×10^{-2}	5.48×10^{-2}	8.12×10^{-2}		
SL(.15,.1,50,100)	2.38×10^{4}	1.13×10^{9}	8.03×10^{13}	7.62×10^{18}	9.04×10^{23}	1.29×10^{29}	2.36×10^{4}	1.01
	2.38×10^{4}	1.13×10^{9}	8.02×10^{3}	7.59×10^{18}	8.98×10^{23}	1.27×10^{29}		
	0	0	-1.37×10^{-3}	-3.41×10^{-3}	-6.09×10^{-3}	-9.33×10^{-3}		

In each rectangle, first entry is k^{th} moment of $f_i(t)$, second entry is k^{th} moment of h(t), and third entry is the relative error.

TABLE 2.4 Compares true values of τ_i and σ_i with simulated estimates $\hat{\tau}_i$ and $\hat{\sigma}_i$.

		10	20	30	40	50
SL(.12, .1, i, 100)	τ_i	3.70×10^2	4.38×10^2	4.60×10^2	4.71×10^2	4.77×10^2
	$\hat{\tau}_i$	3.14×10^2	4.37×10^2	5.51×10^2	3.87×10^2	5.15×10^2
	σ_i	3.69×10^2	3.75×10^2	3.75×10^2	3.75×10^2	3.75×10^2
	$\hat{\sigma}_i$	2.39×10^2	3.03×10^2	4.75×10^2	2.68×10^2	3.79×10^2
SL(.15, .1, i, 100)	τ_i	2.28×10^4	2.37×10^4	2.38×10^4	2.38×10^4	2.38×10^4
	$\hat{\tau}_i$	2.53×10^4	2.81×10^4	1.89×10^4	2.30×10^4	2.75×10^4
	σ_i	2.37×10^4	2.37×10^4	2.37×10^4	2.37×10^4	2.37×10^4
	$\hat{\sigma}_i$	2.05×10^4	2.57×10^4	1.69×10^4	2.45×10^4	2.83×10^4

TABLE 2.5

Values of μ_Q, σ_Q and Q_1 for distribution $\{Q_j\}$ and also $(\mu Q_1)^{-1} = \tau$ for cases SL(λ, .1, i, 100), λ = .15, .16, ..., .20.

λ	μ_Q	σ_Q	Q_1	$(\mu Q_1)^{-1}$
.15	3.09×10^{1}	8.73	4.22×10^{-4}	2.37×10^{4}
.16	3.56×10^{1}	8.31	6.04×10^{-5}	1.66×10^{5}
.17	3.96×10^{1}	7.97	7.30×10^{-6}	1.37×10^{6}
.18	4.31×10^{1}	7.69	7.92×10^{-7}	1.26×10^{7}
.19	4.62×10^{1}	7.45	8.03×10^{-8}	1.25×10^{8}
.20	4.89×10^{1}	7.23	7.81×10^{-9}	1.28×10^{9}

TABLE 2.6 Values of τ for various cases of SL(λ, .1, i, N)

λ \ N	200	300	400	500
.15	2.10×10^{7}	2.27×10^{10}	2.63×10^{13}	3.17×10^{16}
.16	1.48×10^{9}	1.58×10^{13}	1.82×10^{17}	2.16×10^{21}
.17	1.35×10^{11}	1.58×10^{16}	1.97×10^{21}	2.55×10^{26}
.18	1.45×10^{13}	1.97×10^{19}	2.85×10^{25}	4.27×10^{31}
.19	1.72×10^{15}	2.81×10^{22}	4.88×10^{29}	8.77×10^{36}
.20	2.16×10^{17}	4.29×10^{25}	9.09×10^{33}	1.98×10^{42}

CHAPTER 3 THE DISTRIBUTION OF STATES AT TIME t

3.1 BRIEF SURVEY OF METHODS

Whereas in the previous chapter we were concerned with the distribution of extinction times in the SL process for an initial state i [*], for which the distribution function is $p_{io}(t)$, attention will now be directed towards the entire distribution of states $\left\{p_{ij}(t)\right\}_{j=o}^{N}$ for all $t \geq 0$. In a sense this is summarised by the partial differential equation 2.1(9), but as pointed out in 2.1, this does not yield an explicit solution for $G_i(z,t)$ and various approximate analytic or numerical methods must therefore be considered.

In the first place, since the analysis of the previous chapter, particularly 2.6, establishes the form of $G_i(z,t)$ along $z=0$, at least to a very good approximation, then together with the obvious boundary conditions $G_i(z,0) = z^i$ and $G_i(1,t) = 1$, for all $t \geq 0$, the numerical integration of 2.1(9) by a standard algorithm can be expected to be a routine matter. This approach which was first sketched out in 2.1 is taken up again in 3.3.

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* Other more general distributions of the initial state could be equally well considered. The methodology of Chapter 2 is not limited to this special case.

In Section 3.4 Laplace Transform methods are employed and full use is made of the numerical inversion technique due to BELLMAN et al.(1966). This method of numerical analysis has been found to be particularly valuable here as in this way it is possible to analyse the process without making excessive demands on computer time. Moreover, it appears to be the only method which links the small and large t solutions discussed later in this chapter.

The small t solution discussed in 3.5 is due essentially to BAILEY (1968). The importance of this result is that it does describe in purely analytic terms the early development of the process. The error term in this solution is $O(N^{-2})$ with the implied constant being, of course, t-dependent. The method could be developed to an $O(N^{-3})$ error term, though the algebraic labour involved would be considerable, and for this reason this is not taken up here.

Finally in 3.6 the methodology of 2.7 is developed further, i.e. the process conditional on non-extinction is considered, to obtain a large t solution approximation for $G_i(z,t)$. Thus we have a range of techniques which between them make possible the accurate numerical determination of any SL process over its entire effective life-span.

In conclusion to this brief summary, it should be remarked that the numerical results given in tabular form at the end of this chapter, derived by the various methods outlined above, agree well in general. In particular, they were found to be entirely consistent in a probabilistic sense with the simulated results which will be discussed in the next section.

3.2 SIMULATION

The basic aim here is to monitor the simulated process at prescribed time instants $t_1, t_2, \ldots, t_K$, say. The choice of these instants will depend primarily on the value of τ_i, the mean time to extinction, (Tables 2.3, 5 and 6), corresponding to the case considered and also, of course, on available computer time.

Suppose, in fact, that L runs of a case are observed and that $x_{i\ell}(t)$ is the realised value of the state variable $X_i(t)$ (*) at time t in the ℓ'th run, $\ell=1,2,\ldots,$ L. Then for large enough K and L it should be possible by means of these KL observations to get a good idea of how the process develops in time and specifically of the form of the distribution of $X_i(t)$.

In particular, if $\mu_i(t)$, $\sigma_i(t)$, $\eta_i(t)$ and $\kappa_i(t)$ are respectively the mean, standard deviation, skewness and kurtosis of the distribution of $X_i(t)$, then the values of these parameters at $t=t_1, t_2, \ldots, t_K$ can be estimated by the corresponding sample statistics thus,

$$m_i(t_k) = \frac{1}{L} \sum_{\ell=1}^{L} x_{i\ell}(t_k) \qquad (1)$$

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* In the previous chapter the state variable was usually denoted by j. The notation $X_i(t)$ is adopted here however to emphasise both t and i dependence. Actually $X_i(t)$ is also dependent on λ, μ and N but to avoid a cumbersome notation symbols such as $X_{i\lambda\mu N}(t)$ will not be used.

$$s_i(t_k) = \sqrt{L^{-1} \sum_{\ell=1}^{L} \left[x_{i\ell}(t) - m_i(t_k)\right]^2} \qquad (2)$$

$$e_i(t_k) = L^{-1} \left[s_i(t_k)\right]^{-3} \sum_{\ell=1}^{L} \left[x_{i\ell}(t_k) - m_i(t_k)\right]^3 \qquad (3)$$

$$k_i(t_k) = L^{-1} \left[s_i(t_k)\right]^{-4} \sum_{\ell=1}^{L} \left[x_{i\ell}(t_k) - m_i(t_k)\right]^4 \qquad (4)$$

Some results are given in Tables 3.1 for the cases SL (λ, .1, 10, 100) where λ = .12, .15 and .2 with L = 50. Note that for λ = .12 effectively the entire history of the process can be monitored by taking $t_k = 10k$ with K = 50, for here $\tau_{10} = 370$ and $\sigma_{10} = 369$, (see Table 2.4).

On the other hand, such a choice of t_k for the case λ = .15 does little more than describe the very early development of the process for here $\tau_{10} = 22800$ and $\sigma_{10} = 23700$. To get a more general view of this case therefore results were also obtained for $t_k = 10k$ with K = 50, and also, and separately, for $t_k = 500k$ with K = 50.

This in turn does not take us very far in the life-history of the process SL (.2, .1, 10, 100) since here τ_{10} is of the order of 10^9. In fact, within normal computer time limits it is quite impossible to simulate this process to anywhere near extinction, in general. Once past the initial build-up period the process will effectively be the process conditional on non-extinction for a very

long time, and in this quasi steady state situation a few widely spaced moments of observation are sufficient therefore. Thus results for $t_k = 5000k$ and $K = 5$ only are shown.

It would now, of course, be possible on the basis of these simulations to construct confidence intervals for $\mu_i(t)$, $\sigma_i(t)$, $\eta_i(t)$ and $\kappa_i(t)$ or any other process parameters of interest, at the prescribed time instants $t_1, t_2, \ldots\ldots, t_K$. A consideration of results of this type, however, is best deferred until the end of the chapter when the discussion of the relevant theory will have been completed and appropriate numerical comparisons can then be made.

Nevertheless from the results of Tables 3.1 it would seem reasonable to infer the following,(*) for $\phi = \lambda/\mu \geqslant 1.2$ and $\mu = 0.1$.

1) There is a range of t, $0 < T_1 \leqslant t \leqslant T_2$, during which $\mu_i(t)$ closely approximates to a constant N_s, independent of i. If $i < N_s$, then, during the interval $0 \leqslant t \leqslant T_1$ of t, $\mu_i(t)$ is a monotonically increasing function of t, and likewise, if $i > N_s$, it is a monotonically decreasing function of t in this interval.

(*) The standard errors of $m_i(t)$ and $s_i(t)$ are, of course, $\sigma_i(t)/\sqrt{L}$ and $\sigma_i(t)/\sqrt{2L}$ respectively. Also it is not difficult to show that the standard errors of $e_i(t)$ and $k_i(t)$ are approximately $\sqrt{\frac{6}{L}}$ and $\sqrt{\frac{24}{L}}$ for a normal parent population. With $L = 50$ therefore fairly tight probability bounds for $\mu_i(t)$, $\sigma_i(t)$, $\eta_i(t)$ and $\kappa_i(t)$ at $t_1, t_2, \ldots\ldots, t_k$ can be obtained.

2) The period of time $T_s = T_2 - T_1$ is a rapidly increasing function of ϕ. For example, it is about 200 for $\phi = 1.2$, $N = 100$, but in the region of 8000 for $\phi = 1.5$, $N = 100$. (The results for SL (.12, .1, 10, N) for N = 100, 200, 300 and 400 shown in Table 3.2, indicate the dependence of T on N.)

Also the ratio T_1/T_s is small and decreases rapidly as ϕ increases.

3) The distribution of states for $T_1 \leqslant t \leqslant T_2$ is effectively stationary and can be satisfactorily approximated by the normal form. This approximation improves as ϕ increases.

4) The quantity N_s is slightly less than the deterministic mean $N_D = N(1 - \rho)$, where $\rho = \mu/\lambda$. In fact, $N_D - N_s > 0$ also depends on ϕ and decreases as ϕ increases.

5) As t increases beyond T_2, $\mu_i(t)$ starts slowly to approach zero. Further $\sigma_i(t)$ increases and the distribution of states departs from the normal form to become increasingly positively skew.

The implication of these results for any realisation of this process is that unless i is near to zero, then with a probability close to 1 the process level will in a short time reach the neighbourhood of N_s. The probability of drifting from this level to the zero state in a small period of time is very small, though eventually, as we now know, the zero state must be reached.

Otherwise, with a probability close to zero the neighbourhood of N_s is never reached, and then extinction is very likely to occur early on.

This may seem intuitively obvious and in any case is a natural conclusion to draw from the results for extinction times summarised at the end of the previous chapter. It can, however, be justified further by a heuristic argument based on the obvious relationship

$$\mu_i(t) = \left[1 - p_{io}(t)\right] \times N_D + p_{io}(t) \times 0 \qquad (5)$$

Thus if there is a period of time during which $p_{io}(t)$ is effectively a small positive constant p_s, say, as is implied by the results of Tables 3.1 and 3.2, then during this period

$$\mu_i(t) \simeq (1 - p_s)N_D \qquad (6)$$

and the right hand side of (6) is thus the quantity N_s referred to previously. Note also that (6) not only shows that N_s is less than N_D by a small amount, but also that as p_s decreases as ϕ $(= \frac{\lambda}{\mu})$ increases, then so will $N_D - N_s = p_s N_D$. A similar argument also applies with regard to N-dependence.

In the general t-dependent situation, however, instead of (6) we have

$$\mu_i(t) = \Big(1 - p_{io}(t)\Big)N_D \qquad (7)$$

and the 'leakage' $N_D - \mu_i(t) = N_D\, p_{io}(t) = L(t)$, say, quantifies the essential difference between the stochastic and deterministic versions of the logistic process. Of course, since extinction is certain in the SL process then $L(t) \to N_D$ as $t \to \infty$.

In the subsequent sections of this chapter where ways of determining the distribution of $X_i(t)$ will be developed, it will be shown that the inferences 1,2,...,5 above are essentially correct.(*)

(*) The question of normality is considered mainly in the next chapter, however.

With this methodology it will be possible, in particular, to quantify terms such as 'rapidly', 'slowly' etc., used in this section, and also other matters alluded to, such as the dependence of T_s on N_s on the process basic parameters i, λ, μ, N.

3.3 NUMERICAL INTEGRATION OF EQUATION 2.1(9)

We now take up again the boundary value problem approach first indicated in 2.1. Recall that in 2.6 it was shown that the density $f_i(t)$ of the time to extinction T_i, for an initial state i, can be well approximated by the gamma density

$$h(t) = \frac{(t/b)^{c-1} e^{-t/b}}{b\Gamma(c)} \qquad (1)$$

by suitable choice of b and c. This approximation improves as ϕ increases and at $\phi = 2$, for example, there is very close agreement between h(t) and $f_i(t)$, $(i \geqslant 10)$ even up to the sixth moment. (See Table 2.3)

On this basis therefore the function

$$H(t) = 0 \quad \text{for } t<0,$$
$$H(t) = \int_0^t h(u)\,du \quad \text{for} \quad t \geqslant 0 \qquad (2)$$

can be expected to provide an extremely close approximation, except possibly for small t, to the distribution function, $F_i(t)$, of T_i and hence as $G_i(0,t) = p_{io}(t) = F_i(t)$, to $G_i(0,t)$ also. In this way therefore $G_1(z,t)$ is determined along the left-hand boundary of the semi-infinite rectangular region, D say, of the z - t plane

defined by $z = 0$, $t = 0$ and $z = 1$.

Integration of 2.1(9) over D from $t = 0$ to a prescribed value of t, $t = t_1$, can then be carried out by using a standard numerical integration algorithm such as, for example, the CRANK-NICHOLSON implicit method. In this case there are no stability or indeed any special numerical analysis problems. Further details about an appropriate choice of mesh size, control of errors etc. are given in Appendix 8.

However, even though we have a 'well-posed' numerical analysis problem here, this approach cannot be recommended as a way of obtaining a complete description of the SL process. There are two objections.

The first is that very large amounts of computer time even for $t_1 = 1000$ are required, and if several values of ϕ and N are to be considered this would have to be the maximum for t_1. For most computer systems, in fact, the maximum possible t_1 would almost certainly have to be considerably less than 1000. Thus as the results of Table 2.1 show the SL process could not be analyzed in this way over its entire effective life-span for any ϕ greater than about 1.2 or 1.3. This is a serious limitation.

The second, and much more serious, objection is that the moments of the distribution $\left\{p_{ij}(t)\right\}_{j=0}^{N}$ must, in this context, necessarily be obtained from $G_i(z,t)$ by some numerical differentiation process, and since in addition this would be carried out at $z = 0$, the left-hand end point of the interval $[0,1]$, then there would bound to be some doubt about the validity of the results so obtained.

Nevertheless, this does not mean that there is no value at all in obtaining $G_i(z,t)$ by numerical integration. On the contrary it was bound to be invaluable as a means of verifying the reliability of the results obtained by Laplace Transform techniques discussed in the next section. In fact the results for $G_i(z,t)$ obtained by the two methods were found to be in almost complete agreement.(*) Some comparisons are given in Table 3.3

3.4 LAPLACE TRANSFORM TECHNIQUES

In 2.2 it was shown in the proof of Theorem 2.1 how a formal solution of the process in terms of the LAPLACE Transforms $\overline{p}_{ij}(s)$ of the probabilities $p_{ij}(t)$ could be obtained. Clearly therefore if an accurate numerical inversion method is available then we have another basis for determining the distribution of $X_i(t)$ for any t. Such an

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(*) The only region of disagreement is where both z and t are small. However as $G_i(0,t)$ is approximated by $H(t)$ as defined in (2), and $h(t)$ was fitted by the method of moments, then such a discrepancy is to be expected. In fact, however, as $G_i(0,t)$ is negligibly small when t is small then in numerical terms this irregularity is of no real consequence.

inversion procedure is provided by the method of BELLMAN et al. (1966) an account of which together with details of its application to the problem here, is given in Appendix 5. Note that by this approach the probabilities $P_{ij}(t)$ are evaluated first and any other quantities of interest that might be required, such as the moments of the distribution of $X_i(t)$, or $G_i(z,t)$ itself, are derived from them, and not the other way round. Thus the need for numerical differentiation is eliminated.

Another impressive feature of the inversion method is the enormous saving in computer time it effects. This is due to the fact that transforming s to s/k essentially extends t to kt. By this simple artifice which requires negligible additional computer time, the SL process can be taken up to t of the order of magnitude of 10^6, a value which would be out of the question by the boundary value approach as described in the previous section. By that method the amount of CP time required to reach such large values of t would be increased by a factor of about 10^5 as compared with the inversion method.(∇)

(*) The word 'almost' in this context is meant to imply that there is a limit to what can be achieved in this way. If s/k becomes too small the the inversion procedure may become unreliable. This is discussed further in Appendix 5 along with other questions of accuracy, and the use of subsidiary techniques to reduce error.

(∇) See appendices 6 and 8.

One must conclude therefore that the LAPLACE Transform approach both in terms of speed and accuracy is greatly superior to the numerical integration method of the previous section.

Some results for $\mu_i(t)$ and $\sigma_i(t)$ for SL(λ, .1, 10, 100) where λ = .12, .15 and .2 are shown in Tables 3.4 along with some values of $\mu^L(t)$ and $\sigma^L(t)$ the corresponding values derived from the 'large t' solution of 3.6 at the end of this chapter. See also Figs. 3.1, 3.2 and 3.3 which show graphically the dependence of $\mu_i(t)$ on i, and also its closeness to $\mu^L(t)$.

Two further matters call for special comment.

The first is that in view of Theorem 2.1 it is known that each $p_{ij}(t)$ is a linear combination of negative exponentials, $e^{-\alpha t}$. But as independent calculations showed the numerical inversion of $(s + \alpha)^{-1}$ to $e^{-\alpha t}$ can be achieved with great accuracy by BELLMAN's method, the relative error being found to be of the order of 10^{-6}. Thus if $N = 100$ then the relative error for each $p_{ij}(t)$ obtained in this way can be expected to be of the order of 10^{-4}.

Secondly even though, as already pointed out, there is some limit, depending essentially on ϕ, to the maximum t up to which the SL process can be analysed reliably by BELLMAN's method, nevertheless the analysis can easily be completed if necessary by use of the large t solution described in 3.6. In fact the two methods overlap substantially and are in close agreement as is clear from Table 3.4, and Figs. 3.1, 3.2 and 3.3.

3.5 THE SMALL t SOLUTION

An approximate solution for the MGF, $M(\theta,t)$, [*] of the distribution of $X_i(t)$ will now be derived by a method which is due essentially to BAILEY (1968). The solution is approximate in the sense of small t and large N. In this sense $M'(\theta,t)$ is shown to be a perturbation of $m(\theta,t)$ the MGF of the deterministic process which is characterised by the differential equation

$$\frac{dx}{dt} = \lambda x(1 - x) - \mu x \qquad (1)$$

subject to $x(0) = x_o$, say, where $M'(\theta,t)$ is the MGF of the normalised random variable $X_i(t)/N$.

Strictly, of course, the state variable y, $(y = 0, 1, 2, \ldots, N)$, of the deterministic logistic (L) process is discrete, and x as defined by (1) is therefore a continuous approximation to the normalised discrete variable of y/N.

Equation (1) can be rewritten as

$$\frac{dx}{dt} = kx - \lambda x^2 \qquad (2)$$

where $k = \lambda - \mu$, and it is then easy to show that

$$x(t) = 1/(a + be^{-kt}) \qquad (3)$$

where $a = \lambda/k$ and $b = 1/x_o - \lambda/k$.

(*) Although it would be consistent to use $M_i(\theta,t)$ to denote the MGF, corresponding to the PGF $G_i(z,t)$, the form $M(\theta,t)$ will be adopted in order to simplify the notation.

Thus with x(t) determined then, trivially, so is m(θ,t) by

$$m(\theta,t) = e^{\theta x(t)} \tag{4}$$

The SL and L processes can then be compared by considering the partial differential equations which their respective MGF's satisfy. For the L process it is easily shown from (2) and (4) that it is

$$\frac{\partial m}{\partial t} = \theta\left(k\frac{\partial m}{\partial \theta} - \frac{\partial^2 m}{\partial \theta^2}\right) \tag{5}$$

For the SL process it was shown in Section 2.1 to be

$$\frac{\partial M}{\partial t} = \left(e^{\theta} - 1\right)\left(\lambda - \mu e^{-\theta}\right)\frac{\partial M}{\partial \theta} - \frac{\lambda}{N}\left(e^{\theta} - 1\right)\frac{\partial^2 M}{\partial \theta^2} \tag{6}$$

To compare (5) and (6) first put $N\theta = \theta'$ to obtain

$$\frac{\partial M}{\partial t} = N\left(e^{\theta'/N} - 1\right)\left(\lambda - \mu e^{-\theta'/N}\right)\frac{\partial M'}{\partial \theta'} - \lambda N\left(e^{\theta'/N} - 1\right)\frac{\partial^2 M'}{\partial \theta'^2} \tag{7}$$

and hence within $O(N^{-2})$ we have

$$\frac{\partial M'}{\partial t} = \theta'\left(k + \frac{h\theta}{2N}\right)\frac{\partial M'}{\partial \theta'} - \lambda\theta'\left(1 + \frac{\theta'}{2N}\right)\frac{\partial^2 M'}{\partial \theta'^2} \tag{8}$$

where $h = \lambda + \mu$.

For large N therefore (8) can be regarded as a perturbed form of (5), the perturbation terms being $O(N^{-1})$. Thus in this way the eigen function expansion of M' approximates to that for m.

The expansion of m is obtained by putting $m = e^{\omega t}g(\theta)$ in (5) to get

$$\theta\left(\lambda\frac{d^2 g}{d\theta^2} - k\frac{dg}{d\theta}\right) + \omega g = 0 \tag{9}$$

and hence $$\psi\left(\frac{d^2g_1}{d\psi^2} - \frac{dg_1}{d\psi}\right) + \beta g_1 = 0 \qquad (10)$$

where $\psi = \alpha\theta$, $\alpha = 1 - \rho$, $\rho = \mu/\lambda$, $\beta = \omega/\lambda\alpha = \omega/k$, and

$$g_1(\psi) = g(\psi/\alpha).$$

Now provided β is a non-negative integer, j say, the generalised LAGUERRE polynomial $L_j^{(\zeta)}(\psi)$ will satisfy the second order differential equation

$$\psi\frac{d^2g_1}{d\psi^2} + (1 + \zeta - \psi)\frac{dg_1}{d\psi} + \beta g_1 = 0 \qquad (11)$$

where $\zeta > -1$. (See ABROMOWITZ and STEGUN, p. 781).

Thus $m(\theta,t) \equiv m = \lim_{\zeta \to -1} m^{(\zeta)}$ where

$$m^{(\zeta)} = \sum_{j=0}^{\infty} a_j e^{kjt} L_j^{(\zeta)}(\alpha\theta) \qquad (12)$$

where a_j are constants to be determined. This can be effected, in the usual way, by using the orthogonality relationship

$$\int_0^{\infty} e^{-\psi}\psi^{\zeta} L_j^{(\zeta)}(\psi) L_k^{(\zeta)}(\psi)\,d\psi = \frac{\Gamma(\zeta + j + 1)}{j!}\delta_{jk} \qquad (13)$$

where δ_{jk} is KRONECKER's delta.

Multiplication of (12) therefore by $(\alpha\theta)^{\zeta} e^{-\alpha\theta} L_k^{(\zeta)}(\alpha\theta)$, followed by integration with respect to θ over the range $[0,\infty)$ yields

$$a_j = \frac{\alpha^j!\, e^{-kjt}}{\Gamma(\zeta + j + 1)} \int_0^\infty e^{-\theta v(t)} (\alpha\theta)^\zeta L_j^{(\zeta)}(\alpha\theta)\, d\theta \qquad (14)$$

where $$v(t) = \alpha - x(t) = \frac{be^{-kt}}{a(a + be^{-kt})} \qquad (15)$$

Now it is also known (see e.g. ERDE'LYI (1954), § 4.11) that

$$\int_0^\infty e^{-q\psi}\, \psi^\zeta\, L_j^{(\zeta)}(\psi) d\psi = \frac{\Gamma(\zeta + j + 1)}{j!} \cdot \frac{(q - 1)^j}{q^{\zeta+j+1}}, (q > 0) \qquad (16)$$

and application of this result to the integral on the right hand side of (14) leads therefore to

$$a_j = e^{-kjt} \left(v(t)/\alpha - 1\right)^j \left(\alpha/v(t)\right)^{\zeta+j+1} \qquad (17)$$

Note that the condition $q > 0$ in (16) implies here that $v(t) > 0$ for all $t \geqslant 0$ and hence in particular that $v(0) > 0$. Now $v(0) = \frac{b}{a(a + b)}$, so that with reference to (3) we must assume in the subsequent analysis that $x_0 < 1 - \rho$, i.e. that the process starts below the equilibrium level of the L process. Clearly, in practical terms, this is not a limitation of much consequence.

Continuing on this basis therefore put $t = 0$ in (17) to obtain

$$a_j = \left(\frac{v(0)}{\alpha} - 1\right)^j \left(\frac{\alpha}{v(0)}\right)^{\zeta+j+1} \qquad (18)$$

which, using (15), can be shown to be equivalent to

$$a_j = \left(-\frac{\lambda x_o}{k}\right)^j \left(\frac{k}{k - \lambda x_o}\right)^{\zeta+j+1} \tag{19}$$

Hence the eigen function expansion of $m^{(\zeta)}$ is

$$\left(\frac{k}{k - \lambda x_o}\right)^{\zeta+1} \sum_{j=o}^{\infty} (-1)^j \left(\frac{\lambda x_o}{k - \lambda x_o}\right)^j e^{kjt} L_j^{(\zeta)}(\alpha\theta) \quad (*) \tag{20}$$

The equivalence of (20) to $m(\theta,t)$ as defined by (3) and (4) can be shown by using the generating function.

$$(1 - z)^{-\zeta-1} \exp\left(\frac{z\theta}{z - 1}\right) = \sum_{j=o}^{\infty} L_j^{(\zeta)}(\theta)\, z^j. \tag{21}$$

Thus taking $z = \lambda x_o e^{kt}/(\lambda x_o - k)$ we have

$$\sum_{j=0}^{\infty} \left(-\frac{\lambda x_o}{k - \lambda x_o}\right)^j e^{kjt} L_j^{(\zeta)}(\alpha\theta)$$

$$= \left(1 + \frac{\lambda x_o e^{kt}}{k - \lambda x_o}\right)^{-\zeta-1} \exp\left[\frac{x_o k\theta}{\lambda x_o + (k-\lambda x_o)e^{-kt}}\right] \tag{22}$$

and combining (20) and (22) one obtains

$$m^{(\zeta)} = \left(\frac{k}{\lambda x_o(e^{kt} - 1) + k}\right)^{\zeta+1} \exp\left[\frac{x_o k\theta}{\lambda x_o + (k - \lambda x_o)e^{-kt}}\right] \tag{23}$$

Thus let $\zeta \to -1$, and it follows at once that the form (4) is recovered, which completes the verification.

(*) The question of convergence is discussed at the end of this section.

The next stage of the argument is to obtain the eigen function expansion for $M'(\theta,t)$ corresponding to (20). Formally, we put $M' = e^{\Omega t}G(\theta)$ in (8), (θ' is now changed to θ to facilitate comparisons), to obtain the second order differential equation for G, namely

$$\theta\left(k + \frac{h\theta}{2N}\right)\frac{dG}{d\theta} - \lambda\theta\left(1 + \frac{\theta}{2N}\right)\frac{d^2G}{d\theta^2} = \Omega G \qquad (24)$$

corresponding to equation (9) for g. The equation corresponding to (10) is then

$$\psi\left((1 + p\psi)\frac{d^2G_1}{d\psi^2} - (1 + q\psi)\frac{dG_1}{d\psi}\right) + BG_1 = 0 \qquad (25)$$

where $G_1(\psi) = G(\psi/\alpha)$, $p = 1/2\alpha N$ and $q = h/2\alpha kN$, and $B = \Omega/\lambda\alpha = \Omega/k$, and thus parallel to (11) the equation

$$\psi(1 + p\psi)\frac{d^2G_1}{d\psi^2} + (1 + \zeta - \psi)(1 + q\psi)\frac{dG_1}{d\psi} + BG_1 = 0 \qquad (26)$$

is obtained, which reduces to (25) as $\zeta \to -1$.

Now define the operator

$$D_0 \equiv \psi\frac{d^2}{d\psi^2} + (1 + \zeta - \psi)\frac{d}{d\psi} \qquad (27)$$

so that (11) can be written as

$$D_0 g_1 = -\beta g_1 \qquad (28)$$

Also define the operator

$$D \equiv \psi(1 + p\psi)\frac{d^2}{d\psi^2} + (1 + \zeta - \psi)(1 + q\psi)\frac{d}{d\psi} \qquad (29)$$

(p and q defined after equation (25)), and then

$$D = D_0 + N^{-1}D_1 \qquad (30)$$

where

$$D_1 = \frac{\psi^2}{2\alpha}\cdot\frac{d^2}{d\psi^2} + \frac{h\psi(1 + \zeta - \psi)}{2\alpha k}\cdot\frac{d}{d\psi} \qquad (31)$$

Thus equation (26) can now be written as

$$DG_1 = - BG_1 \tag{32}$$

which is the perturbed form of (28). Hence we infer that

$$M'(\theta,t) = \lim_{\zeta \to -1} M''^{(\zeta)}(\theta,t) \tag{33}$$

where $$M'^{(\zeta)}(\theta,t) = \sum_{j=0}^{\infty} A_j e^{\Omega j t} G_{ij}(\alpha\theta) \tag{34}$$

and where the Ω_j and $G_{1j}(\alpha\theta)$ are perturbations of the eigen values kj and the eigen functions $L_J^{(\zeta)}(\alpha\theta)$, respectively, of (12).

Thus write

$$B_j = \beta_j + N^{-1}\varepsilon_j \tag{35}$$

and $$G_{1j} = g_{1j} + N^{-1}\eta_j^{(*)} \tag{36}$$

where $\beta_j = j$, $B_j = \Omega_j/k$ and $g_{1j}(.) \equiv L_j^{(\zeta)}(.)$.

Using (35) and (36) therefore in conjunction with (30) and (32), we have for all j,

$$(D_0 + N^{-1}D_1)(g_{1j} + N^{-1}\eta_j) = - (\beta_j + N^{-1}\varepsilon_j)(g_{1j} + N^{-1}\eta_j) \tag{37}$$

which in view of (28), after neglecting $O(N^{-2})$ terms and multiplying through by N reduces to

$$(D_0 + b_j)\eta_j + (D_1 + \varepsilon_j)g_{1j} = 0 \tag{38}$$

(*) Thus the η_j are functions of ψ. Again, however, to simplify notation we do not write $g_{1j}(\psi)$ etc. On the other hand, $\varepsilon_j = N(B_j - \beta_j)$ is not a function of ψ at all. Essentially it is a measure of the difference between corresponding eigen values of the two partial differential equations (5) and (8) and depends on λ, μ, ζ and j.

Now express the function η_j as linear combinations of the original eigen functions g_{1j}, thus

$$\eta_j = \sum_{k=0}^{\infty} c_{jk} g_{1k} \tag{39}$$

i.e. we assume that the η_j belong to the space spanned by the functions $\left\{g_{1j}\right\}_{j=0}^{\infty}$. Substituting (39) in (38), therefore, and using (28) one readily obtains

$$\sum_{k=0}^{\infty} c_{jk}(b_j - b_k) g_{1k} + (D_1 + \varepsilon_j) g_{1j} = 0 \tag{40}$$

which, since $g_{1j}(\psi) \equiv L_j^{(\zeta)}(\psi)$ and $b_j = j$ is equivalent to

$$(D_1 + \varepsilon_j) L_j^{(\zeta)} + \sum_{k=0}^{\infty} c_{jk}(j - k) L_k^{(\zeta)} = 0 \tag{41}$$

where $L_j^{(\zeta)} \equiv L_j^{(\zeta)}(\psi)$.

Further from (11) and the definition of the operator D_1 in (31), we can write

$$D_1\left(L_j^{(\zeta)}\right) = \ell_j - \frac{j\psi}{2\alpha} L_j^{(\zeta)} \tag{42}$$

where

$$\ell_j^{(\zeta)} \equiv \ell_j^{(\zeta)}(\psi) \equiv \frac{\lambda\mu\psi}{k^2}(1 + \zeta - \psi)\frac{dL_j^{(\zeta)}}{d\psi} \tag{43}$$

and thus (41) can be written in the form

$$\sum_{k=0}^{\infty} (j - k) c_{jk} g_{1k} + \left(\varepsilon_j - \frac{j\psi}{2\alpha}\right) g_{1j} = -\ell_j^{(\zeta)} \tag{44}$$

Multiplying (44) therefore by $e^{-\psi}\psi^{\zeta}.L_m^{(\zeta)}$ and integrating with respect to ψ over the range $[0,\infty)$ one obtains using the orthogonality relationships (13) that

$$(j - m)c_{jm}\gamma_m^{(\zeta)} + \varepsilon_j\gamma_m^{(\zeta)}\delta_{jm} = \frac{j}{2\alpha}\left\{\psi L_m^{(\zeta)}, L_j^{(\zeta)}\right\} - \left\{L_m^{(\zeta)}, \ell_j^{(\zeta)}\right\} \tag{45}$$

where the functional $\{f, g\}$ is defined as

$$\int_0^\infty e^{-\psi}\psi^{\zeta} f(\psi)g(\psi)d\psi .$$

and $$\gamma_m^{(\zeta)} = \frac{\Gamma(m + \zeta + 1)}{m!}.$$

The following standard results for generalised LAGUERRE polynomials $L_j^{(\zeta)} \equiv L_j^{(\zeta)}(\psi)$ will be required.

$$\psi \frac{dL_j^{(\zeta)}}{d\psi} = jL_j^{(\zeta)} - (j + \zeta)L_{j-1}^{(\zeta)} \tag{46}$$

and $$(j + 1)L_{j+1}^{(\zeta)} = (2j + \zeta + 1 - \psi)L_j^{(\zeta)} - (j + \zeta)L_{j-1}^{(\zeta)} \tag{47}$$

(ABRAMOWITZ and SEGUN, Chapter 22).

Clearly (47) can be written as

$$\psi L_j^{(\zeta)} = - (j + 1)L_{j+1}^{(\zeta)} + (2j + \zeta + 1)L_j^{(\zeta)} - (j + \zeta)L_{j-1}^{(\zeta)}. \tag{48}$$

Hence substituting for $\ell_j^{(\zeta)}$ in (45), by means of (43), and using also (46) and (48), we have

$$(j - m)c_{jm}\gamma_m^{(\zeta)} + \varepsilon_j\gamma_m^{(\zeta)}\delta_{jm} = \frac{j}{2\alpha} I_1 - I_2 \tag{49}$$

where $$I_1 = - \frac{j(j + 1)}{2\alpha} \left\{L_{j+1}^{(\zeta)}, L_m^{(\zeta)}\right\} + \frac{j}{2\alpha} (2j + \zeta + 1) \left\{L_j^{(\zeta)}, L_m^{(\zeta)}\right\}$$

$$- \frac{j(j + \zeta)}{2\alpha} \left\{L_{j-1}^{(\zeta)}, L_m^{(\zeta)}\right\} \tag{50}$$

and $$I_2 = \frac{\lambda\mu}{k^2} (1 + \zeta)I_3 - \frac{\lambda\mu}{k^2} I_4 \tag{51}$$

where $$I_3 = \left\{\psi \frac{dL_j^{(\zeta)}}{d\psi}, L_m^{(\zeta)}\right\}$$

$$= \left\{jL_j^{(\zeta)} - (j + \zeta)L_{j-1}^{(\zeta)}, L_m^{(\zeta)}\right\} \tag{52}$$

and
$$I_4 = \left\{ \psi^2 \frac{dL_j^{(\zeta)}}{d\psi} , L_m^{(\zeta)} \right\}$$
$$= \left\{ j\psi L_j^{(\zeta)} - (j + \zeta)\psi L_{j-1}^{(\zeta)}, L_m^{(\zeta)} \right\}. \qquad (53)$$
$$= - j(j + 1)\left\{ L_{j+1}^{(\zeta)}, L_m^{(\zeta)} \right\} + j(2j + \zeta 1)\left\{ L_j^{(\zeta)}, L_m^{(\zeta)} \right\}$$
$$- j(j + \zeta)\left\{ L_{j-1}^{(\zeta)}, L_m^{(\zeta)} \right\} + j(j + \zeta)\left\{ L_j^{(\zeta)}, L_m^{(\zeta)} \right\}$$
$$- (j + \zeta)(2j + \zeta - 1)\left\{ L_{j-1}^{(\zeta)}, L_m^{(\zeta)} \right\}$$
$$+ (j + \zeta)(j + \zeta - 1)\left\{ L_{j-2}^{(\zeta)}, L_m^{(\zeta)} \right\}. \qquad (54)$$

Using again the orthogonality relationship (13) therefore, (49) reduces to

$$(j - m)c_{jm} + \varepsilon_j \delta_{jm} =$$
$$\frac{\lambda\mu}{k^2}\Big(- j(j + 1)\delta_{m,j+1} + j(2j + \zeta + 1)\delta_{mj} - j(j + \zeta)\delta_{j-1,m}$$
$$+ j(j + \zeta)\delta_{mj} - (j + \zeta)(2j + \zeta - 1)\delta_{m,j-1}$$
$$+ (j + \zeta)(j + \zeta - 1)\delta_{m,j-2}\Big)$$
$$- \frac{\lambda\mu(1 + \zeta)}{k^2}\Big(j\delta_{mj} - (j + \zeta)\delta_{j-1,m}\Big)$$
$$+ \frac{j}{2\alpha}\Big(- (j + 1)\delta_{m,j+1} + (2j + \zeta + 1)\delta_{mj} - (j + \zeta)\delta_{m,j-1}\Big) \qquad (55)$$

Since m is an arbitrary non - negative integer the equation (55), though complicated, is sufficient for the determination both of the c's and of the ε's. In fact, put m = j and we obtain at once that

$$\varepsilon_j = \frac{\lambda\mu}{k^2}\Big(j(2j + \zeta + 1) + j(j + \zeta)\Big)$$
$$- \frac{\lambda\mu(1 + \zeta)j}{k^2} + \frac{j}{2\alpha}(2j + \zeta + 1) \qquad (56)$$

For the c's it is obvious from (55) that $c_{mj} = 0$ if either $m > j + 1$ or $m < j - 2$. Otherwise put $m = j - 2$, $j - 1$ and $j + 1$ successively and we have,

$$c_{j,j-2} = \frac{\lambda\mu}{2k^2}(j + \zeta)(j + \zeta - 1) \tag{57}$$

$$c_{j,j-1} = -\frac{\lambda\mu}{k^2}(j + \zeta)(3j + \zeta - 1) + \frac{\lambda\mu}{k^2}(j + \zeta)(1 + \zeta) - \frac{j(j + \zeta)}{2\alpha}$$

$$= \frac{1}{2\alpha k}(j + \zeta)(4\mu - h'j) \tag{58}$$

where $h' = \lambda + 5\mu$

and $$c_{j,j+1} = \frac{\lambda\mu}{k^2} j(j + 1) + \frac{j(j + 1)}{2\alpha} = \frac{h}{2\alpha k} j(j + 1). \tag{59}$$

This leaves c_{jj} to be determined. To effect this put $t = 0$ in (34) and use (36) to obtain

$$e^{x_0\theta} = \sum_{k=0}^{\infty} A_k G_{1k} = \sum_{k=0}^{\infty} A_k (g_{1k} + N^{-1}\eta_k). \tag{60}$$

But we also have by putting $t = 0$ in (12) that

$$e^{x_0\theta} = \sum_{k=0}^{\infty} a_k L_k^{(\zeta)} \tag{61}$$

so that $$\sum_{k=0}^{\infty} a_k L_k^{(\zeta)} = \sum_{k=0}^{\infty} A_k \left(L_k^{(\zeta)} + N^{-1}\eta_k\right) \tag{62}$$

Clearly (62) is satisfied by

$$A_j = a_j \quad \text{for all } j, \text{ and } \sum_{k=0}^{\infty} A_k \eta_k = 0 \tag{63}$$

Thus using (39) we now have

$$\sum_{k=0}^{\infty}\sum_{m=0}^{\infty} a_k c_{km} L_m^{(\zeta)} = 0 \tag{64}$$

which, again using (13), reduces to

$$\sum_{k=0}^{\infty} a_k c_{kj} = 0 \quad \text{for } j = 0, 1, 2, \ldots \tag{65}$$

and therefore to

$$\sum_{k=j-1}^{j+2} a_k c_{kj} = 0. \tag{66}$$

Hence using the result (19) for the a_k in (66) it follows that

$$c_{jj} = d^{-1} c_{j-1,j} + d c_{j+1,j} - d^2 c_{j+2,j} \tag{67}$$

where $d = a/b = \lambda x_0/(k - \lambda x_0)$.

It only remains therefore to assemble (57), (58), and (59) with (67) into a single result for c_{jj}, and after some algebra we obtain

$$c_{jj} = \frac{1}{2\alpha k d}\left[hj(j-1) - d^2(j+\zeta+1)(h+h'j) - \mu d^3(j+\zeta+1)(j+\zeta+2)\right] \tag{68}$$

The functions η_j can now be obtained at once from (39) which reduces to

$$\eta_j = c_{j,j-2} g_{1,j-2} + c_{j,j-1} g_{1,j-1} + c_{jj} g_{1j} + c_{j,j+1} g_{1,j+1} \tag{69}$$

and using (57), (58), (59) and (68) an explicit result for η_j could be formulated if necessary.

We are now therefore in a position to get an approximate result for $M'(\zeta)$, and hence for M'. From (12), (34), (35) and (36) we have

$$M'(\zeta) = \sum_j a_j \exp\left[kt(j + N^{-1}\varepsilon_j)\right](g_{1j} + N^{-1}\eta_j)$$

$$\doteq \sum_j a_j e^{kjt}\left[g_{ij} + N^{-1}(k g_{1j}\varepsilon_j t + \eta_j)\right] + O(N^{-2}) \tag{70}$$

and so

$$M'(\zeta) = m(\zeta) + N^{-1} s(\zeta) + O(N^{-2}) \tag{71}$$

where $$S^{(\zeta)} = \sum_{j=0}^{\infty} a_j e^{kjt} (k\varepsilon_j g_{1j} t + \eta_j) \tag{72}$$

Hence combining (69) and (72) it follows that

$$S^{(\zeta)} = \sum_{j=0}^{\infty} a_j e^{kjt} \Big(k\varepsilon_j g_{1j} t + c_{j,j-2} g_{1,j-2} + c_{j,j-1} g_{1,j-1} + c_{jj} g_{1j} + c_{j,j+1} g_{1,j+1} \Big) \tag{73}$$

$$= \sum_{j=0}^{\infty} \Big(k a_j \varepsilon_j t e^{kjt} + a_{j-1} c_{j-1,j} e^{k(j-1)t} + a_j c_{jj} e^{kjt} + a_{j+1} c_{j+1,j} e^{k(j+1)t} + c_{j+2,j} a_{j+2} e^{k(j+2)t} \Big) g_{1j} \tag{74}$$

or $$S^{(\zeta)} = \sum_{j=0}^{\infty} (-1)^j d^j H^{(\zeta)} W_j^{(\zeta)}(t) L_j^{(\zeta)} e^{kjt} \tag{75}$$

where $$H^{(\zeta)} = \left(\frac{k}{k - \lambda x_o} \right)^{\zeta+1}$$

and $$W_j^{(\zeta)}(t) = k\varepsilon_j t - d^{-1} c_{j-1,j} e^{-kt} + c_{jj} - dc_{j+1,j} e^{kt} + d^2 c_{j+2,j} e^{2kt}. \tag{76}$$

Now from (56), (57), (58), (59) and (68) we have

$$\left.\begin{aligned} \lim_{\zeta \to -1} \varepsilon_j &= \frac{\mu}{\alpha k} (3j - j^2) + \frac{j^2}{\alpha}, \\ \lim_{\zeta \to -1} c_{j,j-2} &= \frac{\mu}{2\alpha k} (j - 1)(j - 2), \\ \lim_{\zeta \to -1} c_{j,j-1} &= \frac{1}{2\alpha k} (j - 1)(4\mu - h'j), \\ \lim_{\zeta \to -1} c_{j,j+1} &= \frac{h}{2\alpha k} j(j + 1), \\ \lim_{\zeta \to -1} c_{jj} &= \frac{1}{2\alpha k d} \left[hj(j - 1) - d^2 j(h + h'j) - \mu d^3 j(j + 1) \right] \end{aligned}\right] \tag{77}$$

Thus $$\lim_{\zeta\to-1} W^{(\zeta)} = Q(t)j + R(t)j^2 \tag{78}$$

where $$Q(t) = -\frac{1}{2\alpha kd}(h + hd^2 + \mu d^3) - \frac{\mu t}{\alpha}$$

$$+ \frac{h}{2\alpha kd} e^{-kt} + \frac{dh}{2\alpha k} e^{kt} + \frac{\mu d^2}{2\alpha k} e^{2kt} \tag{79}$$

and $$R(t) = \frac{1}{2\alpha kd}(h - h'd^2 - \mu d^3) + \frac{\lambda + 2\mu}{\alpha} t$$

$$- \frac{h}{2\alpha kd} e^{-kt} + \frac{dh'}{2\alpha k} e^{kt} + \frac{\mu d^2}{2\alpha k} e^{2kt}. \tag{80}$$

Now from (75) and (76) we have

$$S^{(\zeta)} \equiv S^{(\zeta)}(\psi) = H^{(\zeta)} \sum_{j=0}^{\infty} (-1)^j d^j e^{kjt} \left[Q^{(\zeta)}(t) j \right.$$

$$\left. + R^{(\zeta)}(t) j^2 \right] L_j^{(\zeta)}(\psi) \tag{81}$$

where $Q^{(\zeta)}(t)$ and $R^{(\zeta)}(t)$ are such that $\lim_{\zeta\to-1} Q^{(\zeta)}(t) = Q(t)$ and $\lim_{\zeta\to-1} R^{(\zeta)}(t) = R(t)$. (The functions $Q^{(\zeta)}(t)$ and $R^{(\zeta)}(t)$ are complicated, but it is not necessary for the purposes of this argument to exhibit them explicitly. Only their limits as $\zeta\to-1$ are required.)

To obtain the final result note that (81) can be written as

$$S^{(\zeta)}(\psi) = H^{(\zeta)} \left[k^{-1} Q^{(\zeta)}(t) \frac{\partial}{\partial t} + k^{-2} R^{(\zeta)}(t) \frac{\partial^2}{\partial t^2} \right] K^{(\zeta)}(\psi, t) \tag{82}$$

where $$K^{(\zeta)}(\psi, t) = \sum_{j=0}^{\infty} (-d)^j e^{kjt} L_j^{(\zeta)}(\psi)$$

which by (20) is equal to $\left(\frac{k - \lambda x_0}{k} \right)^{\zeta+1} m^{(\zeta)}(\theta, t)$.

Thus combining (71) and (82) and letting $\zeta\to-1$ we have

$$M'(\theta, t) = m(\theta, t) + N^{-1} \left[k^{-1} Q(t) \frac{\partial}{\partial t} + k^{-2} R(t) \frac{\partial^2}{\partial t^2} \right] m(\theta, t) + O(N^{-2}) \tag{83}$$

The formula (83) can be checked in various ways. Firstly, since as may be easily verified $Q(0) = R(0) = 0$, then it is clear that $M'(\theta,0) = m(\theta,0)$, as of course should be the case. Also putting $\theta = 0$, it will readily be found that the fundamental condition $M'(0,t) \equiv 1$ is satisfied. Thus so is $M(0,t) \equiv 1$.

It is also possible to verify the correctness of (83) as $N \to \infty$. A cursory inspection might suggest that the limit of $M'(\theta,t)$ as $N \to \infty$ is $m(\theta,t)$, an obviously erroneous conclusion. However, to investigate correctly the limiting behaviour of (83) as $N \to \infty$, so as to compare, for example, expressions for the mean and variance obtained in this way with those of the unrestricted process, we must regard i as fixed and hence i/N as tending to zero as $N \to \infty$. In this sense it is possible to show, after some laborious algebra, that

$$\left.\begin{aligned} Q(t) &= -\frac{h}{2\lambda\alpha x_o}(1 - e^{-kt}) + O(1) \\ \text{and} \qquad R(t) &= \frac{h}{2\lambda\alpha x_0}(1 - e^{-kt}) + O(1) \end{aligned}\right] \tag{84}$$

the constants implied by the order notation being t - dependent.

Also in the same way it is possible to show from (3) that

$$x = x_0 e^{kt} - \frac{\lambda x_0^2}{k} e^{kt}(e^{kt} - 1) + O(x_0^3) \tag{85}$$

and thus that

$$\left[-k^{-1}\frac{\partial}{\partial t} + k^{-2}\frac{\partial^2}{\partial t^2}\right] m(\theta,t) = \left[-k^{-1}\theta\dot{x} + k^{-2}(\theta^2\dot{x}^2 + \theta\ddot{x})\right] e^{\theta x}$$

$$= x_0^2 e^{2kt}(\theta^2 - 2\lambda k^{-1}\theta) e^{\theta x} + O(x_o^3) \tag{86}$$

Hence from (83),(84) and (86) we have

$$M'(\theta,t) = m(\theta,t) + \frac{hx_0}{2\lambda\alpha N}(e^{2kt} - e^{kt})(\theta^2 - 2\lambda k^{-1}\theta)e^{\theta x} + O(x_o^3) \qquad (87)$$

and thus by replacing θ by $N\theta$ it follows that(*)

$$M(\theta,t) = m_y(\theta,t) + \frac{hi}{2\lambda\alpha}(e^{2kt} - e^{kt})(\theta^2 - 2\lambda\theta k^{-1}N^{-1})\, e^{\theta y} + O(N^{-2}) \qquad (88)$$

where,it will be recalled, $y \equiv y(t)$ is the non - normalised variable Nx of the L process and $m_y(\theta,t) = e^{\theta y(t)}$ is the corresponding MGF.

Therefore, if we now differentiate $M(\theta,t)$ as defined by (88), once and twice with respect to θ, and set $\theta = 0$ etc., then in the usual way we will obtain

$$\mu_i(t) = y(t) - \frac{hi}{k\alpha N}(e^{2kt} - e^{kt}) + O(N^{-2}) \qquad (89)$$

$$\sigma^2(t) = \frac{ki}{\lambda\alpha}\left(e^{2kt} - e^{kt}\right) + \frac{2hiy}{k\alpha N}\left(e^{2kt} - e^{kt}\right)\left(e^{2kt} - e^{kt} - 1\right) + O(N^{-2}) \qquad (90)$$

Thus as $y(t) \to ie^{kt}$ as $N \to \infty$, then

$$\lim_{N\to\infty} \mu_i(t) = ie^{kt} \qquad (91)$$

and $$\lim_{N\to\infty} \sigma_i^2(t) = \frac{hi}{\lambda\alpha} e^{kt}(e^{kt} - 1) = \frac{i(\lambda + \mu)}{\lambda - \mu} e^{kt}(e^{kt} - 1) \qquad (92)$$

showing agreement with the standard results for the birth - death process for which $\lambda_n = \lambda n$ and $\mu_n = \mu n$, i.e. for the unrestricted process.

It should be emphasised that (89) and (90) are not, in general, reliable as computational formulae. Their only, and essential purpose is to show the correct limiting form of $\mu_i^s(t)$ and $\sigma_i^s(t)$, the small t

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(*) A detailed consideration of the form of the implied constant in the error term in (87) will show that this changes to $O(N^{-2})$ and not $O(N^{-3})$ in passing to (88).

approximations of $\mu_i(t)$ and $\sigma_i(t)$ respectively, as derived from (83) when $N \to \infty$. In fact the numerical results for $\mu_i^s(t)$ and $\sigma_i^s(t)$ exhibited in Table 3.5 are based on (83), neglecting the error term, and no further approximations are made. Clearly there is good agreement between these values and the corresponding results obtained by the LAPLACE Transform method provided, of course, t is sufficiently small.

Thus there remains the question as to what is the maximum value of t, t_s say, up to which the results for $\mu_i^s(t)$ and $\sigma_i^s(t)$ are reliable. The results obtained here suggest that t_s could depend on some or all of the basic parameters λ, μ, i and N.

In attempting an answer to this question an obvious starting point is to consider the series (20). This is convergent if $t < t_c$, say, where

$$t_c = k^{-1} \ln\left[\frac{k}{\lambda x_0} - 1\right] \qquad (93)$$

Since necessarily $t > 0$, then the condition (93) implies that $x_0 < \frac{k}{2\lambda}$, i.e. the process level must initially be less than half way below the equilibrium level. In practical terms, however, this is not a serious limitation.

Moreover, the results of Table 3.5 show that, in fact, t_s can be in excess of t_c. Thus, for example, for SL(.15, .1, 10, 100), $t_c = 16.9$ yet the relative error for values of $\mu_i^s(t)$ and $\sigma_i^s(t)$ as compared with $\mu_i(t)$ and $\sigma_i(t)$ is less than about 10% even at t = 40. Further, for SL(.12, .1, 5, 100), $t_c = 42.4$ and for SL(.2, .1, 10, 100), $t_c = 13.9$ and satisfactory results, though not so impressive as when $\lambda = .15$, are obtained beyond this value of t.

3.6 THE LARGE t SOLUTION

In contrast to the heavy analysis of the previous section, the obtaining of a large t solution for $G_i(z,t)$, and hence for $\mu_i(t)$ and $\sigma_i(t)$ is formally a simple matter. Thus if $G_Q(z)$ is the PGF of the distribution $\Pi_Q \equiv \left\{ Q_i \right\}_{i=1}^{N}$, defined in Section 2.7 as the distribution of states conditional on non - extinction, then for large t

$$G_i(z,t) = p_{i0}(t) \times 1 + \left[1 - p_{i0}(t)\right] \times G_Q(z) \qquad (1)$$

and so by equation 2.7(12)

$$G_i(z,t) \simeq (1 - e^{-\mu Q_1 t}) + e^{-\mu Q_1 t} G_Q(z) \equiv G^{(L)}(z,t), \text{ say.} \qquad (2)$$

In particular, from (2) we have immediately that

$$\mu^L(t) = e^{-\mu Q_1 t} \sum_{j=1}^{N} jQ_j \qquad (3)$$

and

$$\left[\sigma^L(t)\right]^2 = e^{-\mu Q_1 t} \sum_{j=1}^{N} j(j-1)Q_j + \mu^L(t)\left[1 - \mu^L(t)\right] \qquad (4)$$

as large t approximations for $\mu_i(t)$ and $\sigma_i(t)$ respectively.

As already pointed out, the evaluation of the Q's is a routine matter with the aid of a computer, and so therefore will be the evaluation of formulae such as (2), (3) and (4). Note that these formulae show that the large t solution is independent of i, thus theoretically $\mu_i(t)/\mu^L(t) \to 1$ as $t \to \infty$ whatever the value of i. Nevertheless, as Figs. 3.1, 3.2 and 3.3 indicate, the accuracy of the large t solution for a given t improves the nearer i is to the mean of the distribution Π_Q. In particular, of course, if the initial distribution of states is Π_Q then (2) is exact for all t.

Here, however, we compare in Table 3.4 the numerical results for $\mu^L(t)$ and $\sigma^L(t)$ with those already found for $\mu_i(t)$ and $\sigma_i(t)$ by the LAPLACE Transform method, and as pointed out at the end of Section 3.4 there is a region of good agreement between the results obtained by the two methods.

Table 3.1 (A) SL(.12, .1, 10, 100) i = 10

t	NL	m_i	s_i	e_i	k_i	t	NL	m_i	s_i	e_i	k_i
10	50	9.62	4.03	.25	2.64	20	49	10.1	5.21	.32	3.33
30	47	9.98	5.86	.64	2.90	40	45	10.44	6.82	.74	3.89
50	41	11.1	7.36	.32	2.48	60	41	9.66	7.77	.58	2.96
70	39	8.44	7.72	.89	3.10	80	38	8.84	8.27	.64	2.27
90	36	9.80	9.32	.65	2.26	100	36	10.00	9.02	.38	1.78
110	34	10.14	8.56	.36	2.08	120	33	9.48	8.92	.51	2.11
130	33	8.96	8.74	.59	2.19	140	33	8.74	8.71	.71	2.41
150	33	8.74	10.48	1.16	3.30	160	33	7.56	8.31	1.11	4.04
170	29	8.16	8.35	.64	2.31	180	28	7.28	9.14	1.04	2.89
190	27	7.74	9.88	1.35	4.67	200	26	6.70	8.79	1.26	3.75
210	24	6.38	8.73	1.41	4.66	220	23	6.42	9.21	1.51	4.66
230	23	6.44	9.86	1.66	4.99	240	23	6.08	8.53	1.38	4.08
250	21	5.58	7.84	1.15	3.02	260	21	5.38	7.76	1.23	3.19
270	21	5.90	8.50	1.19	3.08	280	21	6.62	9.98	1.41	3.88
290	21	6.78	9.90	1.17	2.89	300	20	6.10	9.18	1.18	2.86
310	19	6.28	9.26	1.13	2.95	320	17	5.34	8.62	1.43	3.78
330	17	5.20	8.59	1.37	3.31	340	17	4.98	8.11	1.30	3.13
350	16	4.32	7.17	1.32	3.11	360	15	4.26	7.07	1.22	2.74
370	14	4.84	8.45	1.48	3.69	380	14	3.56	6.38	1.98	5.98
390	13	3.18	6.14	1.89	5.41	400	13	3.14	6.66	2.26	7.12
410	13	3.54	7.24	2.18	6.99	420	13	4.08	8.67	2.25	7.23
430	12	3.98	8.06	1.93	5.54	440	12	4.06	8.27	1.81	4.64
450	12	3.34	6.92	1.98	5.83	460	12	3.18	6.41	2.04	6.34
470	12	2.94	5.90	1.93	5.69	480	12	3.66	7.44	1.81	4.84
490	11	3.44	6.70	1.59	3.88	500	11	3.10	6.47	1.86	4.88

Values of m_i, s_i, e_i and k_i are based on 50 runs. Also NL equals number of those runs which have not reached the zero state at the current value of t. Similarly for Tables 3.1(B),(C) and (D).

Table 3.1 (B) SL (.15, .1, 10, 100)

t	NL	m_i	s_i	e_i	k_i	t	NL	m_i	s_i	e_i	k_i
10	50	13.36	5.81	.98	4.57	20	49	15.94	7.39	.66	3.59
30	49	19.24	9.90	.46	2.76	40	49	21.18	8.46	- .37	2.70
50	49	22.56	8.65	- .37	3.18	60	49	24.96	10.26	- .23	3.58
70	48	26.10	9.75	- .39	2.80	80	48	28.22	10.50	- .77	3.30
90	48	30.36	10.54	- .80	4.20	100	48	29.40	10.32	- .76	3.71
110	48	30.42	11.03	- .62	3.80	120	48	30.34	10.32	- .88	4.06
130	48	29.30	9.95	- .67	4.53	140	48	27.96	8.92	-1.19	5.00
150	48	28.14	10.01	- .78	4.03	160	48	28.96	9.37	-1.08	4.56
170	48	28.70	10.13	- .70	3.63	180	48	28.56	9.26	-1.01	4.58
190	48	27.16	9.74	- .86	3.71	200	48	27.52	10.23	- .64	3.41
210	48	29.66	10.58	- .84	3.71	220	48	30.38	10.73	- .62	4.02
230	48	29.98	10.19	- .97	4.05	240	48	30.24	10.43	- .48	4.48
250	48	29.98	9.91	- .96	4.34	260	48	29.76	9.36	-1.27	5.00
270	48	29.64	10.22	- .81	4.18	280	48	30.02	10.70	- .68	3.68
290	48	30.72	10.39	- .98	4.17	300	48	29.18	10.56	- .82	3.47
310	48	29.28	11.79	- .62	3.08	320	48	28.30	12.19	- .24	3.10
330	48	28.54	11.88	- .62	2.88	340	48	28.60	11.81	- .51	3.09
350	48	28.54	10.40	- .97	3.95	360	48	30.16	11.24	- .59	3.88
370	48	29.70	11.38	- .93	3.41	380	48	30.28	10.90	- .90	3.72
390	48	29.60	10.23	- .90	3.71	400	48	27.96	10.60	- .53	3.19
410	48	28.70	10.93	- .64	2.90	420	48	29.54	9.87	-1.12	4.36
430	48	28.84	11.01	- .54	3.49	440	48	29.40	10.94	- .49	3.58
450	48	29.20	10.49	-1.20	4.12	460	48	29.22	10.52	- .84	3.65
470	48	29.28	10.92	-.75	3.75	480	48	28.06	10.99	- .63	3.19
490	47	28.64	9.56	- .85	4.00	500	47	28.78	10.14	-1.13	4.50

Table 3.1(C) SL(.15, .1, 10, 100)

t/100	NL	m_i	s_i	e_i	k_i	t/100	NL	m_i	s_i	e_i	k_i
5	48	31.04	7.85	- .16	2.61	10	48	27.88	9.73	- .72	3.97
15	46	29.84	9.51	-1.04	4.79	20	46	27.06	10.28	-1.32	4.38
25	46	28.44	12.16	- .68	3.20	30	46	26.80	10.20	-1.16	4.37
35	45	27.98	11.74	-1.07	3.83	40	45	27.68	12.33	- .96	3.23
45	43	26.72	11.39	-1.37	3.90	50	43	24.76	12.86	- .63	2.57
55	43	25.92	13.04	- .76	2.79	60	43	26.86	13.20	- .86	2.95
65	43	25.62	12.82	-1.00	2.74	70	43	26.86	12.63	-1.04	3.25
75	42	25.74	13.42	- .69	2.80	80	40	25.10	13.48	- .80	2.43
85	38	24.00	14.79	- .47	2.24	90	38	25.24	17.06	- .25	1.87
95	38	24.06	15.38	- .48	2.08	100	38	23.92	15.67	- .34	2.08
105	38	23.40	14.64	- .56	2.10	110	38	24.68	15.72	- .52	1.95
115	38	23.32	14.79	- .53	1.97	120	38	22.50	13.93	- .61	2.11
125	38	23.14	15.36	- .42	1.80	130	36	21.42	14.61	- .31	1.75
135	36	23.98	16.81	- .44	1.62	140	33	22.12	15.25	- .44	1.74
145	30	19.58	16.55	- .11	1.37	150	30	18.68	16.68	.02	1.39
155	30	19.14	16.76	- .06	1.31	160	29	19.52	17.67	- .02	1.29
165	27	15.40	14.81	.22	1.64	170	27	17.16	16.79	.16	1.40
175	26	17.34	18.07	.30	1.47	180	26	16.86	17.25	.24	1.37
185	26	15.88	16.09	.22	1.45	190	26	16.38	16.83	.25	1.37
195	26	15.48	16.45	.43	1.68	200	25	16.06	16.75	.30	1.43
205	25	14.38	15.78	.47	1.67	210	24	15.16	16.30	.30	1.39
215	23	14.28	16.19	.40	1.40	220	23	14.70	16.71	.42	1.46
225	23	15.08	17.34	.48	1.57	230	23	15.04	17.70	.63	1.96
235	23	13.94	16.40	.59	1.80	240	23	14.20	17.50	.59	1.74
245	22	13.76	16.43	.52	1.53	250	22	15.02	17.95	.48	1.39

Table 3.1 (D) SL(.2, .1, 10, 100)

t	NL	m_i	s_i	e_i	k_i
5000	50	47.00	7.96	- .37	2.61
10000	50	48.98	7.76	.42	3.11
15000	50	47.58	7.04	.21	2.48
20000	50	47.48	7.48	.15	2.04
25000	50	47.90	7.30	- .12	2.51

Table 3.2

m_i v t for N=100, 200, 300, 400
for SL(.12, .1, 100, N)

t	N=100 m_i	N=200 m_i	N=300 m_i	N=400 m_i	t	N=100 m_i	N=200 m_i	N=300 m_i	N=400 m_i
20	10.1	12.18	12.60	13.48	40	10.44	15.50	18.28	18.46
60	9.66	17.20	23.26	20.82	80	8.84	17.62	27.16	22.52
100	10.00	16.14	29.50	28.72	120	9.48	17.22	30.40	30.32
140	8.74	15.78	31.76	32.94	160	7.56	15.16	33.84	32.54
180	7.28	14.08	34.06	35.12	200	6.70	15.06	37.80	36.90
220	6.42	16.36	38.94	34.52	240	6.08	14.84	40.88	36.38
260	5.38	15.24	37.68	39.18	280	6.62	16.42	37.98	38.92
300	6.10	15.66	37.10	40.14	320	5.34	16.22	34.72	39.60
340	4.98	14.48	30.12	40.20	360	4.26	13.92	33.36	41.22
380	3.56	14.70	32.64	40.90	400	3.14	15.04	37.20	40.28
420	4.08	15.36	36.42	40.60	440	4.06	15.70	33.60	38.78
460	3.18	14.92	35.54	40.60	480	3.66	15.26	35.30	42.72
500	3.10	15.16	34.52	42.14	-	-	-	-	-

Table 3.3

Compares values of $G_i(z,t)$ obtained by numerical integration with those obtained by Laplace Transform methods for SL(λ .1,10,100) at t=10, 50, 100.

λ	z = .2	z = .4	z = .6	z = .8	z = .9	
.12	2.06×10^{-3} 2.85×10^{-3}	6.72×10^{-3} 7.61×10^{-3}	2.72×10^{-2} 2.81×10^{-2}	1.41×10^{-1} 1.42×10^{-1}	3.60×10^{-1} 3.61×10^{-1}	t=10
.15	9.39×10^{-4} 1.06×10^{-3}	3.10×10^{-3} 3.22×10^{-3}	1.37×10^{-2} 1.38×10^{-2}	8.99×10^{-2} 8.98×10^{-2}	2.78×10^{-1} 2.78×10^{-1}	t=10
.2	2.50×10^{-4} 2.53×10^{-4}	7.80×10^{-4} 7.85×10^{-4}	3.76×10^{-3} 3.75×10^{-3}	3.62×10^{-2} 3.60×10^{-2}	1.63×10^{-1} 1.62×10^{-1}	t=10
.12	1.06×10^{-1} 1.13×10^{-1}	1.20×10^{-1} 1.28×10^{-1}	1.50×10^{-1} 1.58×10^{-1}	2.47×10^{-1} 2.53×10^{-1}	4.13×10^{-1} 4.17×10^{-1}	t=50
.15	2.49×10^{-2} 2.57×10^{-2}	2.73×10^{-2} 2.80×10^{-2}	3.31×10^{-2} 3.36×10^{-2}	5.97×10^{-2} 5.94×10^{-2}	1.49×10^{-1} 1.47×10^{-1}	t=50
.2	1.87×10^{-3} 1.87×10^{-3}	1.92×10^{-3} 1.92×10^{-3}	2.03×10^{-3} 2.03×10^{-3}	2.64×10^{-3} 2.65×10^{-3}	1.40×10^{-2} 1.42×10^{-2}	t=50
.12	2.43×10^{-1} 2.46×10^{-1}	2.53×10^{-1} 2.56×10^{-1}	2.75×10^{-1} 2.78×10^{-1}	3.48×10^{-1} 3.51×10^{-1}	4.81×10^{-1} 4.83×10^{-1}	t=100
.15	3.88×10^{-2} 3.90×10^{-2}	3.95×10^{-2} 3.97×10^{-2}	4.12×10^{-2} 4.14×10^{-2}	5.20×10^{-2} 5.21×10^{-2}	1.10×10^{-1} 1.11×10^{-1}	t=100
.2	1.87×10^{-3} 1.97×10^{-3}	1.92×10^{-3} 1.97×10^{-3}	2.03×10^{-3} 1.97×10^{-3}	2.64×10^{-3} 2.05×10^{-3}	1.40×10^{-2} 9.82×10^{-3}	t=100

In each rectangle, upper number is value of $G_i(z,t)$ obtained by numerical integration.

Table 3.4

Compares $\mu_{10}(t)$ with $\mu^L(t)$ and $\sigma_{10}(t)$ with $\sigma^L(t)$ for SL(λ, .1, 10, 100) where λ = .12, .15 and .2.

	t	0	20	40	60	80	100	200	300	400	500
λ=.12	$\mu_{10}(t)$	10	11.1	11.3	11.3	10.9	10.4	8.1	6.4	4.5	3.5
	$\mu^L(t)$	14.3	13.6	12.8	12.2	11.5	10.9	8.4	6.4	4.9	3.7
	$\sigma_{10}(t)$	0	6.1	7.7	8.5	8.9	9.1	9.3	9.0	8.1	7.3
	$\sigma^L(t)$	8.1	8.5	8.8	9.1	9.2	9.3	9.4	8.9	8.3	7.5

	t	0	50	100	500	1000	5000	10000	20000	30000	40000	50000
λ=.15	$\mu_{10}(t)$	10	24.1	28.4	29.1	28.0	24.0	19.3	12.7	8.4	5.3	3.5
	$\mu^L(t)$	30.9	30.8	30.8	30.3	29.6	25.0	20.3	13.3	8.7	5.7	3.7
	$\sigma_{10}(t)$	0	10.7	10.8	11.2	12.0	15.0	16.4	16.2	14.5	12.0	10.2
	$\sigma^L(t)$	8.7	8.8	8.9	9.7	10.5	14.4	16.3	16.3	14.7	12.6	10.5

	t	0	50	10^2	10^3	10^4	10^5	10^6
λ=.20	$\mu_{10}(t)$	10	46.4	48.8	48.7	48.8	48.8	48.8
	$\mu^L(t)$	48.9	48.9	48.9	48.9	48.9	48.9	48.9
	$\sigma_{10}(t)$	0	8.7	7.6	8.0	7.6	7.6	7.7
	$\sigma^L(t)$	7.2	7.2	7.2	7.2	7.2	7.3	7.4

Table 3.5

Compares $\mu_i(t)^{(*)}$ with $\mu_i^s(t)$ and $\sigma_i(t)^{(*)}$ with $\sigma_i^s(t)$ for SL(.12, .1, 5, 100) and SL(λ, .1, 10, 100) with λ = .15 and .2

	t	0	10	20	30	40	50
λ = .12	$\mu_5(t)$	5.0	5.66	6.21	6.62	6.94	7.13
	$\mu_5^s(t)$	5.0	5.86	6.51	7.05	7.48	7.84
	$\sigma_5(t)$	0.0	3.48	5.00	5.98	6.92	7.51
	$\sigma_5^s(t)$	0	3.50	5.22	6.65	7.85	8.83
λ = .15	$\mu_{10}(t)$	10.0	13.6	17.1	19.9	22.5	24.4
	$\mu_{10}^s(t)$	10.0	13.7	17.4	21.0	24.7	29.3
	$\sigma_{10}(t)$	0	5.57	8.05	9.42	10.4	10.8
	$\sigma_{10}^s(t)$	0	5.57	8.26	9.72	10.2	9.8
λ = .2	$\mu_{10}(t)$	10.0	19.8	30.4	38.6		
	$\mu_{10}^s(t)$	10.0	19.9	31.5	44.1	—	—
	$\sigma_{10}(t)$	0	7.34	10.2	10.5		
	$\sigma_{10}^s(t)$	0	7.42	10.3	9.18		

(*) Values of $\mu_i(t)$ and $\sigma_i(t)$ are obtained by the LAPLACE Transform method.

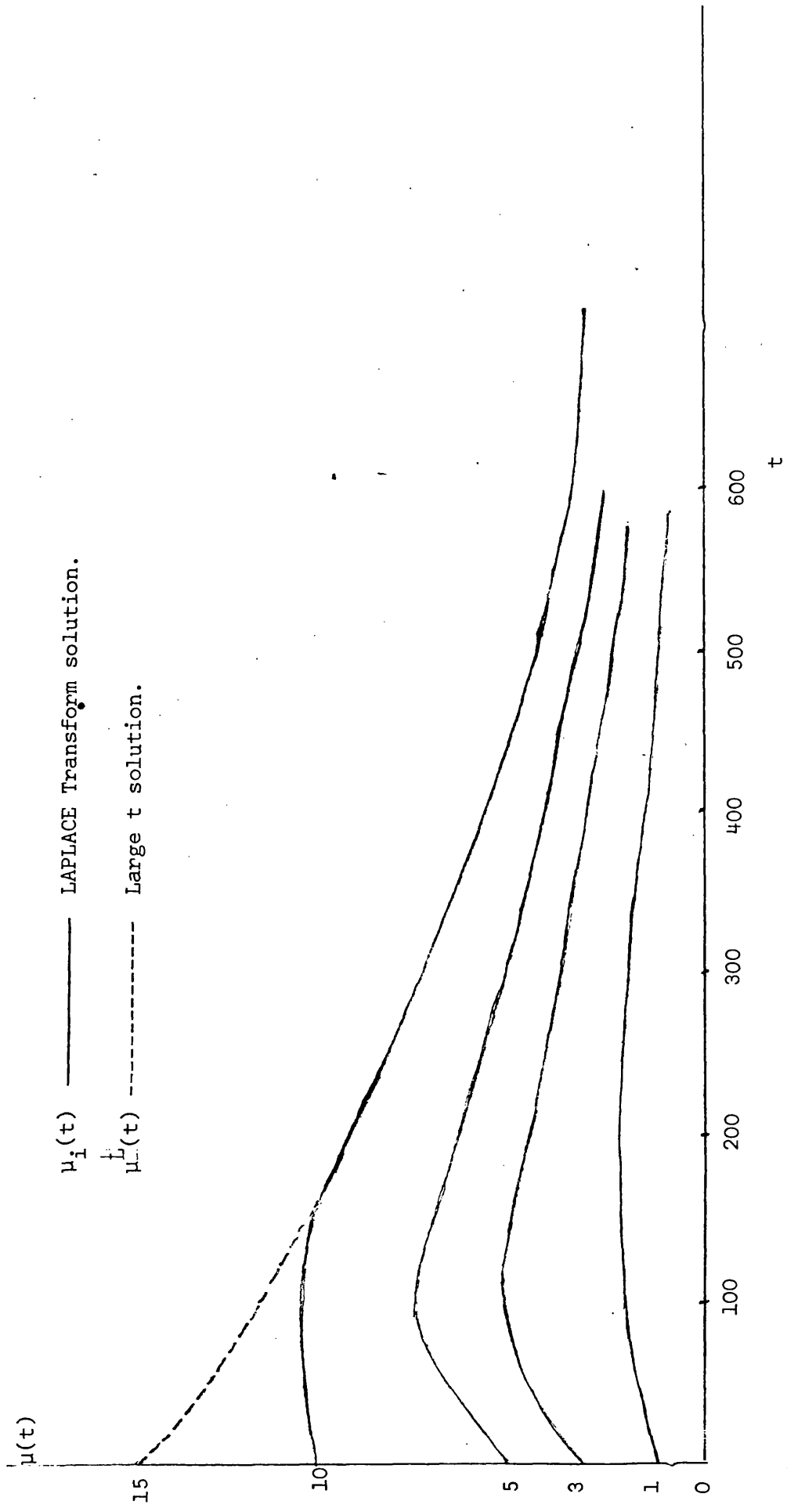
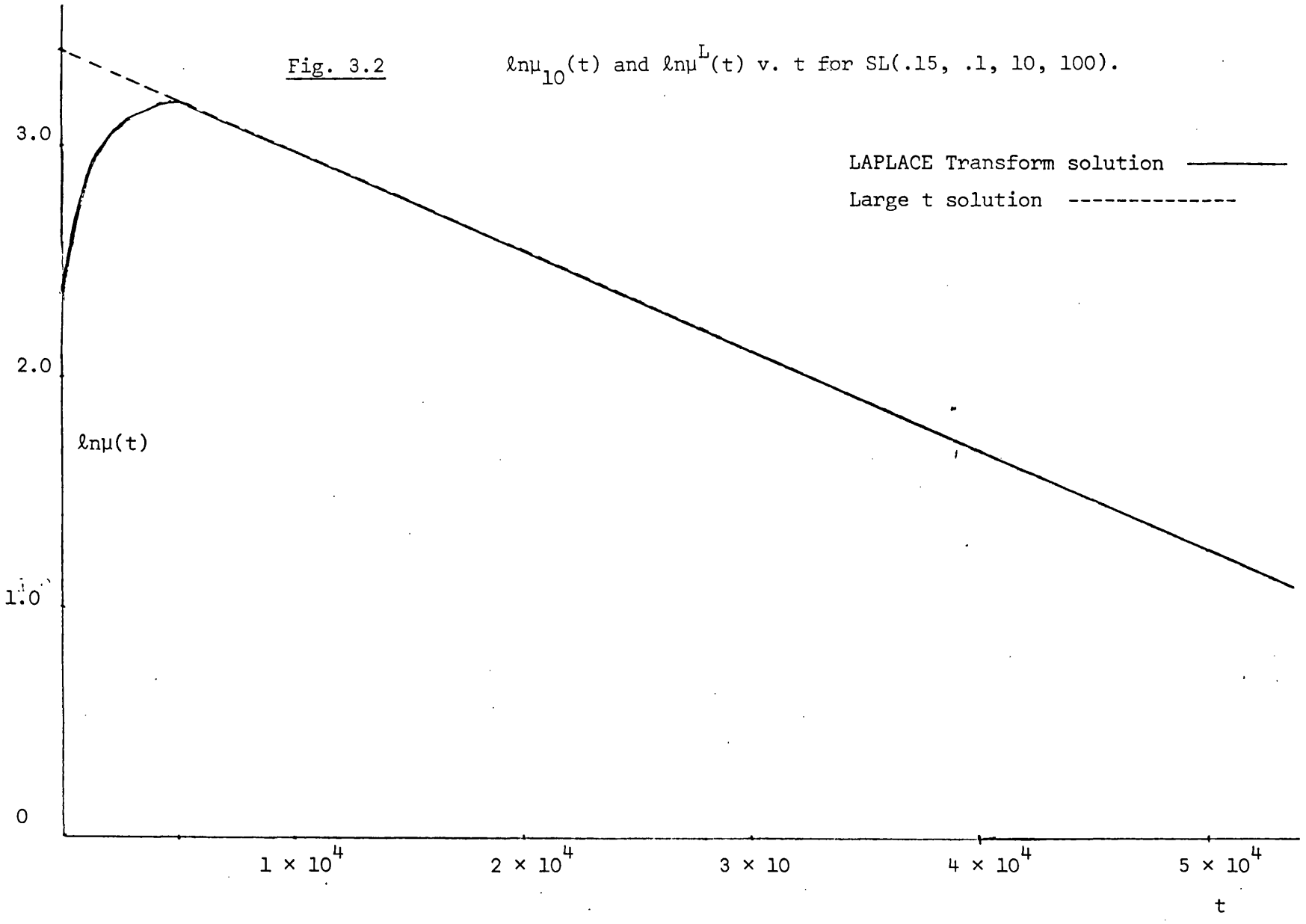


Fig. 3.1 $\mu_i(t)$ and $\mu^L(t)$ v. t for SL(.12, .1, i, 100)

Fig. 3.2 $\ell n\mu_{10}(t)$ and $\ell n\mu^{L}(t)$ v. t for SL(.15, .1, 10, 100).



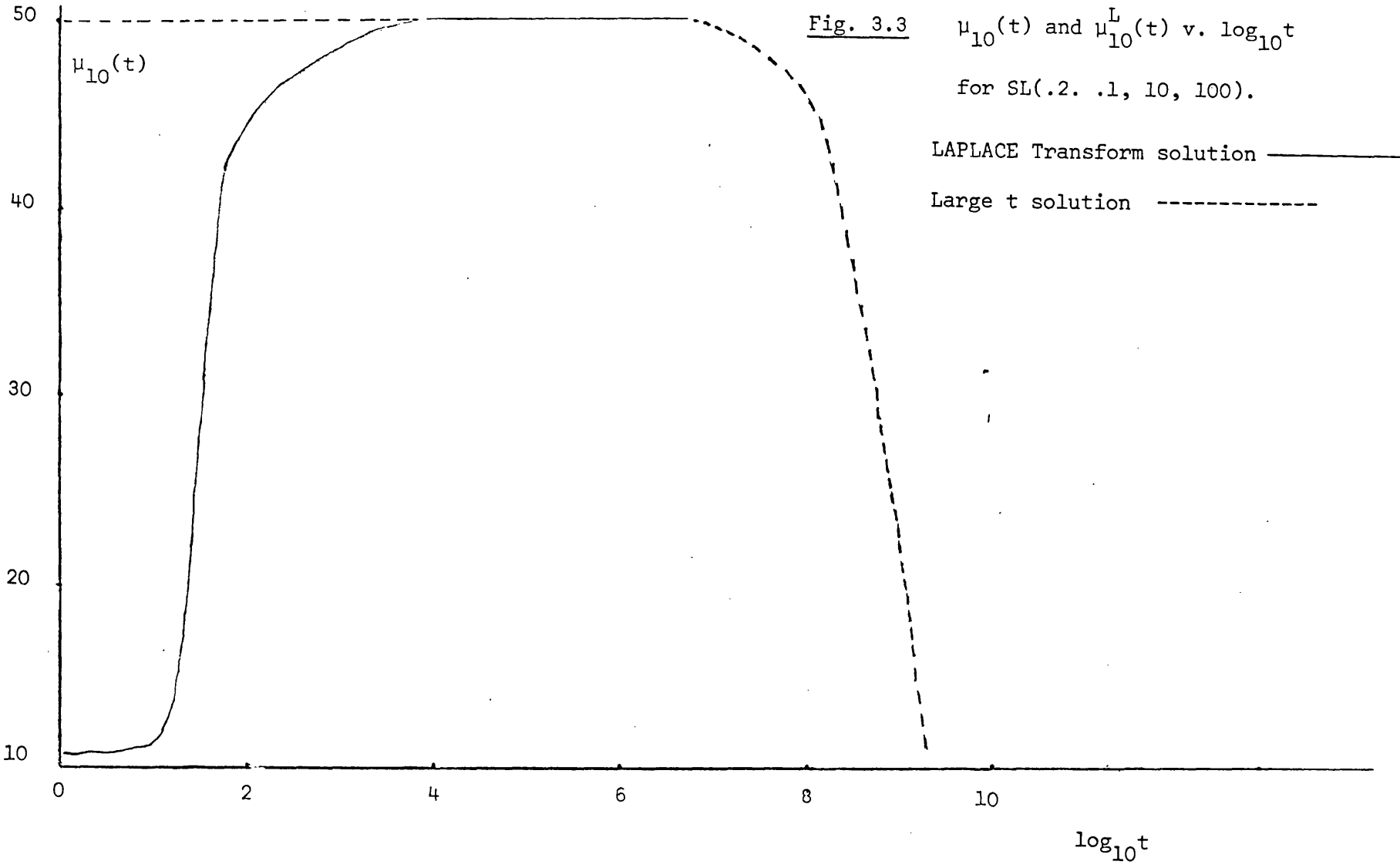


Fig. 3.3 $\mu_{10}(t)$ and $\mu^{L}_{10}(t)$ v. $\log_{10}t$ for SL(.2. .1, 10, 100).

LAPLACE Transform solution ————————.

Large t solution ----------

CHAPTER 4

A DIFFUSION APPROXIMATION OF THE SL PROCESS

4.1 PRELIMINARY REMARKS

So far the numerical evaluation of the SL process has been in terms of N=100. Clearly, however, this value of N is far too small for most ecological situations. Therefore we consider first the possibility of applying the existing methodology with N increased to more realistic values such as 10^3, 10^4 or even 10^6.

Unfortunately, although there is no theoretical limitation in this context to the value of N, this approach will be found to be numerically unworkable for N greater than about 500. The reason for this is that the solution of a system of equations such as 2.2(10) for N of this magnitude will involve very large numbers which will cause computer overflow problems. Actually most computer systems would not go much beyond N=200 in this situation.

Neither does there appear to be any effective method of avoiding this difficulty either by carrying out a suitable transformation of these equations, or by approximating them in some suitable way by a more tractable system. For this reason therefore attention will now be directed towards an analysis of a diffusion approximation to the SL process, and it will thus be shown how the large N situation can be dealt with. In any case, such a diffusion process is of interest in its own right, quite apart from the fact that it will enable us to gain important insights into the SL process itself.

4.2 KOLMOGOROV'S EQUATION FOR THE DIFFUSION APPROXIMATION

Consider therefore rescaling the range of states from $[0,N]$ to $[0,1]$ by the simple transformation $W(t) = X(t)/N$. Thus in this normalised SL (NSL) process each jump is of magnitude $\frac{1}{N}$, and $W(t)$ is limited to the finite set of values $\left\{\frac{j}{N}\right\}_{j=0}^{N}$. Moreover, within $o(\delta t)$ the distribution of $\delta W = W(t+\delta t) - W(t)$, conditional on $W(t) = w$ is as follows.

δw	$-\frac{1}{N}$	0	$\frac{1}{N}$
$P(\delta W = \delta w \mid W = w)$	$\mu_w \delta t$	$1-\lambda_w\delta t-\mu_w\delta t$	$\lambda_w\delta t$

where $\lambda_w = \lambda w(1-w)N$ and $\mu_w = \mu w N$.

Hence

$$\lim_{\delta t\to 0} \frac{E(\delta W \mid W = w)}{\delta t} = \lambda w(1-w) - \mu w$$

and $$\lim_{\delta t\to 0} \frac{V(\delta W \mid W = w)}{\delta t} = \frac{\lambda w(1-w) + \mu w}{N}$$

We consider therefore the diffusion logistic (DL) process with state variable $Y(t)$ on $[0,1]$ for which in the usual terminology (e.g. COX and MILLER (1965), Chapter 5), the infinitesimal mean $\beta(y)$ is given by

$$\beta(y) = \lambda y(1-y) - \mu y \qquad (1)$$

and the infinitesimal variance $\alpha(y)$ by

$$\alpha(y) = \frac{\lambda y(1-y) + \mu y}{N} \qquad (2)$$

Hence if $p(x,y,t)$ is the PDF of $Y(t)$, for $Y(0) = x$, then in the usual way the KOLMOGOROV forward equation for the DL process can be shown to be

$$\frac{\partial^2}{\partial y^2}\left[(a_1 y - b_1 y^2)\, p(x,y,t)\right] - \frac{\partial}{\partial y}\left[(a_2 y - b_2 y^2) p(x,y,t)\right]$$

$$= \frac{\partial p(x,y,t)}{\partial t} \qquad (3)$$

where $a_1 = \frac{\lambda + \mu}{2N}$, $b_1 = \frac{\lambda}{2N}$, $a_2 = \lambda - \mu$ and $b_2 = \lambda$

We now look therefore for methods of solving (3), and related equations, working on the supposition that any results derived from them for the DL process will for large enough N, closely approximate to the corresponding results for the NSL process and hence to the SL process itself.

The question as to how large N must be in order to obtain reliable results for the SL process in this way will become evident later in this chapter. As a very general conclusion, however, it will be found that in terms of increasing N this new methodology may be employed long before the old runs out, and this, of course, is a very satisfactory state of affairs.

To some extent the development of this chapter follows along the same lines as that of the previous chapter, and we consider next therefore mean extinction times of the DL process.

4.3 MEAN OF T(x), THE TIME TO EXTINCTION FOR Y(0) = x

The backward equation corresponding to 4.2 (3) is

$$\tfrac{1}{2}\alpha(x)\frac{\partial^2 p(x,y,t)}{\partial x^2} + \beta(x)\frac{\partial p(x,y,t)}{\partial x} = +\frac{\partial p(x,y,t)}{\partial t} \qquad (1)$$

and from it, following the method of COX and MILLER (Chapter 5), a second order differential equation for $M(x,s) = E\left\{\exp\left[sT(x)\right]\right\}$, the MGF of $T(x)$, can readily be derived.

For if $f(x,t)$ is the PDF of $T(x)$, and $F(x,t)$ the corresponding DF, then

$$P\left[T(x)>t\right] = 1 - F(x,t) = \int_0^1 p(x,y,t)dy$$

so that $$f(x,t) = -\frac{\partial}{\partial t}\int_0^1 p(x,y,t)dy$$

Hence the LAPLACE Transform of (1) leads to the equation

$$\tfrac{1}{2}\alpha(x)\frac{d^2\bar{f}(x,s)}{dx^2} + \beta(x)\frac{d\bar{f}(x,s)}{dx} = + s\bar{f}(x,s) \qquad (2)$$

where $$\bar{f}(x,s) = \int_0^\infty e^{-st}f(x,t)dt.$$

Also since $\bar{f}(x,s) = M(x,-s)$ then

$$\left.\frac{d^\ell f(x,s)}{ds^\ell}\right]_{s=0} = (-1)^\ell \left.\frac{d^\ell M(x,s)}{ds^\ell}\right]_{s=0} = (-1)^\ell m_\ell(x) \qquad (3)$$

where $m_\ell(x)$ is the ℓ^{th} moment of $T(x)$.

Thus differentiating (2) ℓ-times with respect to s, setting s=0, and using (3) we have the system of equations

$$(a_1x - b_1x^2)\frac{d^2m_\ell(x)}{dx^2} + (a_2x - b_2x^2)\frac{dm_\ell(x)}{dx} + \ell m_{\ell-1} = 0 \qquad (4)$$

where $\ell = 1,2,3,\ldots$, and where $m_0(x) \equiv 1$, for all $x > 0$.

In particular if $\ell = 1$, we have

$$(a_1x - b_1x^2)\frac{d^2m}{dx^2} + (a_2x - b_2x^2)\frac{dm}{dx} + 1 = 0 \qquad (5)$$

where $m = m_1(x) = E\left[T(x)\right]$.

Boundary conditions for (5) can be shown to be, by standard arguments, $m(0+) = 0$ and $\left.\frac{dm(x)}{dx}\right]_{x=1} = 0$,

so that m is now uniquely defined.

A formal solution for (5) may easily be derived by elementary methods, and a brief outline of the method of obtaining it is given below.

In the first place, since (5) can be written as

$$\frac{d}{dx}\left[(a_i - b_1x)^{\theta}e^{\phi x}\frac{dm}{dx}\right] + \frac{1}{x}(a_1 - b_1x)^{\theta-1}e^{\phi x} = 0 \qquad (6)$$

where $\theta = 4N\rho$ $(\rho = \mu/\lambda)$, and $\phi = 2N$, then a particular integral of (5) is

$$P(x) = \int_1^x (a_1 - b_1v)^{-\theta}e^{-\phi v}\int_v^1 \frac{1}{u}(a_1 - b_1u)^{\theta-1}e^{\phi u}dudv \qquad (7)$$

Note that $\lim_{x\to 0+} P(x)$ exists for

$$\int_1^x \ell n(v)dv = x\ell m(x) - x + 1 \to 1 \text{ as } x \to 0+.$$

Also a complementary function for (5) can be shown to be

$$C(x) = A + B\int(a_i - b_1x)^{-\theta}e^{-\phi x}dx$$

where A and B are arbitrary constants.

Hence imposing the boundary conditions stated above on the general solution $P(x) + C(x)$ it will be found that

$$m(x) = \int_0^x\int_v^1 g(u,v)\,du\,dv \qquad (8)$$

where $$g(u,v) = \frac{1}{u(a_1 - b_1u)}\left(\frac{a_1 - b_1u}{a_1 - b_1v}\right)^{\theta}e^{\phi(u-v)}$$

Clearly $g(u,v)$ has a singularity at $(0,0)$ in the u-v plane, so that therefore the result (8) regarded as a Reimann double integral is interpreted as

$$\lim_{\delta \to 0} \int_{\delta}^{x} \int_{v}^{1} g(u,v)\,du\,dv \quad . \tag{9}$$

It is easy to show that it is finite, as in view of the results of the previous chpters it must be. However, no simple analytic development of this result appears to be possible so that its evaluation must necessarily involve some numerical integration procedure. With this objective in mind, therefore, it will be found convenient to employ the transformation $u = v + w(1-v)$ to obtain

$$m(x) = \int_0^x \int_0^1 h(v,w)\,dw\,dv \tag{10}$$

where $$h(u,w) = (1 - v)\left[v + w(1 - v)\right]^{-1} (a_1 - b_1 v)^{-\theta}$$

$$\times \left[a_1 - b_1 v - b_1 w\,(1 - v)\right]^{\theta-1} e^{\phi(1 - v)w} \quad .$$

The region of integration is now rectangular. In addition it is necessary to know the form of $h(v,w)$ in the neighbourhood of $(0,0)$ in (v,w) plane. In fact, it can be shown that as $k \to 0$

$$\int_0^k \int_0^k h(v,w)\,dv\,dw = Gk + O(k^2) \tag{11}$$

where G is a complicated function of λ, μ and N, but is independent of k. It is then a simple matter to adapt the numerical integration formula appropriately so as to take the singularity at (0,0) into account. This is discussed further in Appendix 10.

The cases SL(λ,.1,i,N) equivalent to DL(λ,.1,x,N) (*) where λ = .12, .13, .14, .15; i = 10, 20, 30; N = 100, 200, were reconsidered, and results obtained on the basis of (8) appear to agree well with those derived by the method of Section 2.4, as the comparisons exhibited in Tables 4.1 clearly show.

Also values of $m = E[T(x)]$ for DL(λ,.1,x_E, N) where $x_E = 1 - \rho$, the equilibrium level of the DL process, for λ = .105, .110, .115 and for N = 10^3, 10^4, 10^5 are shown in Table 4.2 (†), and are exhibited by graphs of $\log_{10}(\log_{10} m)$ v $\log_{10} N$ in fig. 4.1

In general terms, the importance of these results is that they show the very rapid increase of m with N. In fact, if both $N \geq 10^3$ and $\lambda \geq .11$ (μ = .1), then in ecological terms the mean extinction time is effectively infinite.

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* The notation DL(λ,μ,x,N) will be used to specify cases of the DL process in the same way that SL(λ,μ,i,N) is used for the SL process. Note that x = i/N.

† Actually the case DL(.115, .1, x_E, 10^5) is not included since here m(x) is too large.

4.4 THE HIGHER MOMENTS OF T(x)

For the higher moments the boundary conditions for the system of equations 4.3(4) are $m_\ell(0) = 0$ and $\left.\frac{dm_\ell(x)}{dx}\right]_{x=1} = 0$. It is thus possible following the argument of the previous section to obtain formulae for the $m_\ell(x)$ analogous to 4.3(8). In fact, it will be found that

$$m_\ell(x) = \ell \int_0^x \int_1^v \frac{1}{u(a_1 - b_1 u)} \left(\frac{a_1 - b_1 u}{a_1 - b_1 v}\right)^\theta m_{\ell-1}(u) e^{\phi(u-v)} du\, dv \qquad (1)$$

thus effectively expressing $m_\ell(x)$ as a multiple integral.

The evaluation of $m_\ell(x)$ though likely to make heavy demands on computer time should nevertheless be feasible up to $\ell = 4$ by the use of standard numerical integration procedures for multiple integrals. Cases of larger values of ℓ, however, would probably require excessive computer time.

It will be possible therefore, in principle, to extend the argument of Section 2.6 to the large N situation, and so from $m_1(x)$ and $m_2(x)$ determine the parameters b and c which define the gamma density to which $f(x,t)$ most closely approximates.

4.5 SOME GENERAL COMMENTS ABOUT THE NUMERICAL EVALUATION OF p(x,y,t)

Having got this far it would be a logical step, following the development of the previous chapter, to set up a boundary value problem for the numerical determination of $p(x,y,t)$, using equation 4.2(3), along the lines of Section 3.3. Another possibility would

be to consider the LAPLACE Transform method of BELLMAN et al. Section 3.4, by which a great deal was achieved in the case of the SL process for N = 100, and where it was found to be greatly superior to the boundary value approach both in terms of computer time and accuracy.

In fact, it is easy to show by considering the LAPLACE Transform of equation 4.2(3) and deriving the appropriate boundary conditions that such a method is theoretically feasible. In reality it was found after considering this approach in some detail that there were severe numerical stability problems which could not be resolved satisfactorily, and that therefore reliable results for $p(x,y,t)$ could not be obtained in this way.

However, since, as is now known, in the large N situation extinction times are in general (*) very large, then it is evident that for most cases of interest such a numerical solution will be unnecessary. The reason for this conclusion lies essentially in the fact, as will be shown in the next section, that it is possible to obtain the distribution Π_Q of the state variable Y, conditional on non-extinction, for the DL process.

This in turn, as was shown in Section 3.6 for the SL process, makes possible the determination of the form of the unconditional

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* The qualifying phrase 'in general' means here that extinction times will not be 'very large' when λ is slightly greater than μ as in the case, for example, DL (.101, .1, 1 - ρ, 10^4). We are not here concerned with cases where $\lambda \leq \mu$, where in any case $E[T(x)]$ would not be large.

distribution of Y(t) for large t. Actually if the initial distribution is Π_Q then, of course, the large t solution is exact for all t. (*) If the initial distribution is not Π_Q but the mean extinction time is large, then relatively early on in the life of the process the large t solution can be used to describe the distribution of Y(t). An example of this is shown in fig 3.3 for the case SL(.2, .1, i, 100).

In the exceptional situations where λ is only slightly larger than μ and extinction times are not large therefore, the large t solution will only give a reasonably accurate description of the process towards the end of its life span. If more information about this type of situation is required then recourse to the boundary value approach, or to the LAPLACE Transform methodology, would have to be reconsidered. Another possibility would be to employ the small t solution derived in 3.5.

However, this problem is largely of theoretical interest and its solution would be unlikely to be of much practical value. Thus we infer that for situations of ecological interest where N is large, the large t solution will give a perfectly satisfactory account of the process. It will also become evident in the final section of this

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* In ecological terms an assumed initial distribution Π_Q for the SL process, and hence for the DL process as well, would seem reasonable, if the only available information about the initial population was that it was not extinct.

chapter that the large t solution for the DL process will lead to remarkably simple and informative conclusions about the SL process in general.

4.6 DISTRIBUTION OF STATES CONDITIONAL ON NON-EXTINCTION

The argument here is analogous to that of Section 2.7. Write $g(x,t) = P(T(x) \leq t | x)$ (*) i.e. $g(x,t)$ is the probability that the zero state was reached at or before time t, given that $Y(0) = x$. Let $q(x,y,t)$ be the PDF of the distribution of states Y conditional on non-extinction. Then the densities $p(x,y,t)$ and $q(x,y,t)$ are related by

$$q(x,y,t) = \frac{p(x,y,t)}{1 - g(x,t)} \tag{1}$$

and combining this with 4.2(3) we have the equation

$$\frac{\partial q(x,y,t)}{\partial t} - \frac{q(x,y,t)}{1 - g(x,t)} \frac{\partial g(x,t)}{\partial t}$$

$$= \tfrac{1}{2} \frac{\partial^2}{\partial y^2} \left[\alpha(y) q(x,y,t)\right] - \frac{\partial}{\partial y} \left[\beta(y) q(x,y,t)\right] \tag{2}$$

Further $g(x,t + \delta t) = g(x,t) + p(x,\delta y,t)\mu_{\delta y}.\delta t + o(\delta t)$ (3)

(δy can be interpreted as $\frac{1}{N}$) and thus as $\mu_{\delta y} = \mu.\delta y.N = \mu$ then the limiting form of (3) in the sense of $\delta t \to 0$ is

$$\frac{\partial g(x,t)}{\partial t} = p(x,\delta y,t)\mu_{\delta y} = \mu p(x,\delta y,t). \tag{4}$$

---

* Thus $g(x,t) \equiv F(x,t)$ of Section 4.3.

Hence $$\frac{1}{1 - g(x,t)} \frac{\partial g(x,t)}{\partial t} = \frac{\mu p(x,\delta y,t)}{1 - g(x,t)} = \mu q(x,\delta y,t) \qquad (5)$$

so that (2) now reduces to

$$\frac{\partial q(x,y,t)}{\partial t} - \mu q(x,y,t) q(x,\delta y,t)$$

$$= \frac{1}{2} \frac{\partial^2}{\partial y^2} \left[\alpha(y) q(x,y,t)\right] - \frac{\partial}{\partial y} \left[\beta(y) q(x,y,t)\right] \qquad (6)$$

For large t we have $q(x,y,t) = Q(y)$ the density of the steady state conditional distribution, Π_Q, and thus $\frac{\partial q(x,y,t)}{\partial t} = 0$.

Also as $Q(\delta y) \to 0$ as $\delta y \to 0+$, then we seek a solution of

$$\frac{1}{2} \frac{d^2}{dy^2} \left[\alpha(y) Q(y)\right] - \frac{d}{dy} \left[\beta(y) Q(y)\right] = 0 . \qquad (7)$$

subject to $Q(\varepsilon_N) = 0(\varepsilon_N)$ (8)

and $$\int_{\varepsilon_N}^{1} Q(y)dy = 1 \qquad (9)$$

where $\varepsilon_N \to 0$ as $N \to \infty$, and whose precise form will be determined later.

Using therefore the definitions 4.2(1) and 4.2(2) of $\beta(y)$ and $\alpha(y)$ respectively in (7) it will be found after integrating once and rearranging that

$$\frac{dQ(y)}{dy} = - \left(2N + \frac{1}{y} + \frac{4N\rho - 1}{1 + \rho - y}\right) Q(y) \qquad (10)$$

A further integration will then show that the required density is

$$Q(y) = B_N^{-1} L(y) \quad \text{for} \quad \varepsilon_N \le y \le 1$$
$$= 0 \ , \quad \text{otherwise,} \qquad (11)$$

where $$L(y) = \frac{1}{y} e^{2Ny}(1 + \rho - y)\psi \qquad (12)$$

$\psi = 4N\rho - 1$, and $B_N = \int_{\varepsilon_N}^{1} L(y)dy$.

Now in the interval $(0,1]$ of y, $L(y)$ has one maximum point, at $y = y_1$, and one minimum point, at $y = y_2$, where

$$y_1, y_2 = \frac{1}{2N}\left[1 + N - N\rho \pm \sqrt{N^2(1-\rho)^2 - 4N\rho}\right] \qquad (13)$$

Thus $y_1 = 1 - \rho + O\left(\frac{1}{N}\right)$ and $y_2 = \left(\frac{\rho}{1-\rho}\right)\frac{1}{N} + O\left(N^{-2}\right)$ (14)

so that the appropriate value of ε_N is y_2.

It has therefore been established that $Q(y)$ is unimodal on $\left[\varepsilon_N, 1\right]$. It can also be shown to satisfy condition (8) and, of course, by construction it satisfies (9).

To determine its proximity to the normal form put

$$y = \frac{z}{\sqrt{2N}} + 1 - \rho \qquad (15)$$

and after some algebra it will be found that

$$\ell n\left[L(y)\right] = 2N(1-\rho) + \sqrt{2Nz} - \ell n\left[1 - \rho + \frac{z}{\sqrt{2N}}\right]$$
$$+ (4N\rho - 1)\ \ell n\left[2\rho - \frac{z}{\sqrt{2N}}\right]$$
$$= A(N,\rho) - \frac{z^2}{4\rho} + O(N^{-\frac{1}{2}}) \qquad (16)$$

where $A(N,\rho) = (2N - 1)\ln(1 - \rho) + (4N\rho - 1)\ln 2\rho$ and the constant implied by the order notation is z-dependent.

Hence as $N\to\infty$ the DF of z converges to $\underline{\Phi}\left(\frac{z}{\sqrt{2\rho}}\right)$ where $\underline{\Phi}(.)$ is the DF of a standard normal variate. Thus we have proved the following.

Theorem 4.1

The DF of the conditional distribution Π_Q of Y of the DL process is asymptotic in the sense of $N\to\infty$ to $\underline{\Phi}\left(\frac{y - 1 + \rho}{\sqrt{\rho/N}}\right)$, where $\underline{\Phi}(x) = \left(\frac{1}{\sqrt{2\pi}}\right)\int_{-\infty}^{x} e^{-\frac{u^2}{2}}\,du$

In the limit therefore the distribution Π_Q of the DL process collapses into a unit mass located at $1 - \rho$ in the interval $(0,1]$ of y, i.e. it is located at the equilibrium point.

An alternative and obvious version of Theorem 4.1 as it relates to the SL process is given below.

Theorem 4.2

The DF of the conditional distribution Π_Q of X of the SL process is asymptotic in the sense of $N\to\infty$ to

$$\underline{\Phi}\left(\frac{y - N(1 - \rho)}{\sqrt{\rho N}}\right).$$

If therefore $\mu_N = N(1-\rho)$ and $\sigma_N = \sqrt{\rho N}$, then an immediate corollary of Theorem 4.2 is that both $\eta_N = \mu_N/\mu_Q$ and $\zeta_N = \sigma_N/\sigma_Q$, where μ_Q and σ_Q are respectively the mean and standard deviation of the distribution Π_Q relating to the SL process, tend to 1 as $N\to\infty$. The rapidity with which they do so is indicated by the results of Table 4.3 where the cases $\lambda = .12, .15$ and $.2$, $\mu = .1$ and $N = 200, 300, 400, 500$ are considered. The values of μ_Q and σ_Q are determined from the system of equations 2.7(8), (9) and (10).

4.7 LARGE t SOLUTION

A further implication of Theorem 4.2 is that the MGF, $M_Q(\theta)$, of the distribution Π_Q for the SL process is asymptotic to $\exp\left[N(1-\rho)\theta + \tfrac{1}{2}N\rho\theta^2\right] = M(N,\theta)$, say. More precisely, it can be shown that

$$M(N,\theta)/M_Q(\theta) = 1 + O(N^{-\frac{1}{2}}) \qquad (1)$$

as N tends to infinity.

In place of equation 3.6(2) therefore, it is now possible to write

$$M(\theta,t) \simeq \left(1 - e^{-t/\tau}\right) + e^{-t/\tau} \exp\left[N(1-\rho)\theta + \tfrac{1}{2}N\rho\theta^2\right] \qquad (2)$$

as an approximation for $M(\theta,t)$ the MGF of the distribution of states at time t of the SL process. (*)

Thus from (2) we have

$$\mu(t) \simeq N(1-\rho)e^{-t/\tau} \tag{3}$$

$$\sigma^2(t) \simeq N^2(1-\rho)^2 (e^{-t/\tau} - e^{-2t/\tau}) + \rho N e^{-t/\tau} \tag{4}$$

as approximations to the mean and variance of the distribution of states.

The accuracy of (3) and (4) depend, of course, on λ, μ and N. Its dependence on t increases the more the initial distribution deviates from Π_Q. If the initial distribution is Π_Q which will now be described as defining the standard form of the process for prescribed λ, μ and N, then the error in (3) and (4) is independent of t and depends only on λ, μ and N therefore. In this context the results of Table 4.3 show that if, for example, $\mu = .1$ and $\lambda \geq .15$ then the relative error will be not more than 1% for $N \geq 500$. As λ decreases below .15, however, N would have to be increased beyond 500 if the same accuracy is to be achieved. In fact, extrapolation of the results of Table 4.3 would suggest that if $\lambda = .12$ then a minimum value of N for a maximum relative error of 1% is approximately 1000. On the other hand, if a relative error of 10% can be tolerated then we would only require $N \geq 400$. Clearly this is not an unsatisfactory state of affairs.

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* Note that $\tau = (\mu Q_1)^{-1}$ as proved in Section 2.7

The higher moments can be obtained similarly from (2). For example it can be shown that for $t>0$

$$\mu_3(t) = E\left\{[x(t) - \mu(t)]^3\right\}$$

$$= N^3(1-\rho)^3 e^{-t/\tau}(1 - e^{-t/\tau})(1 - 2e^{-t/\tau}) + O(N^2) \qquad (5)$$

which result enables us to investigate the symmetry of the distribution of states at time t.

In fact, it is now possible to give a simple quantative description of the standard process for large N by means of (3), (4) and (5). To this end it is helpful to regard (4) as

$$\sigma(t) = N(1-\rho)\sqrt{e^{-t/\tau} - e^{-2t/\tau}} + O(\tfrac{1}{N}) \qquad (6)$$

Note the mean reduces to $\frac{1}{2}\mu(0) = \frac{1}{2}N(1-\rho)$ at time $\tau.\ell n 2 = \tau_H$, say, which may thus be described as the <u>half-life</u> of the process. Moreover at $t = \tau_H$, $\sigma(t)$ reaches a maximum value of $\frac{1}{2}N(1-\rho)$ and $\mu_3(t)$ is momentarily zero, i.e. the distribution is symmetric. For $0<t<\tau_H$ the distribution of states is negative skew, and is positive-skew for $t>\tau_H$.

Finally, it is now clear how the standard form of the process may be determined for any large N, for τ can be calculated by the method of Section 4.3. In particular, writing $\nu \equiv \nu(t) \equiv \ell n\, \mu(t)$ then clearly (3) is equivalent to

$$\nu = L - t/\tau \qquad (7)$$

where $L = \ell n[N(1-\rho)]$, so exhibiting a simple linear relationship between ν and t. Some results are shown in Table 4.4.

TABLE 4.1

Mean extinction times computed by the method of Section 2.4 and by the method of Section 4.3 (*).

λ

N	.12	.13	.14	.15	
100	3.70×10^2	1.01×10^3	4.07×10^3	2.28×10^4	x = .1
	3.71×10^2	1.01×10^3	4.02×10^3	2.21×10^4	
200	1.57×10^3	1.67×10^4	4.38×10^5	2.09×10^7	
	1.56×10^3	1.66×10^4	4.23×10^5	1.93×10^7	

N	.12	.13	.14	.15	
100	4.37×10^2	1.14×10^3	4.37×10^3	2.37×10^4	x = .2
	4.39×10^2	1.14×10^3	4.32×10^3	2.29×10^4	
200	1.68×10^3	1.71×10^4	4.41×10^5	2.09×10^7	
	1.68×10^3	1.69×10^4	4.25×10^5	1.93×10^7	

N	.12	.13	.14	.15	
100	4.60×10^2	1.17×10^3	4.42×10^3	2.38×10^4	x = .3
	4.62×10^2	1.17×10^3	4.37×10^3	2.30×10^4	
200	1.71×10^3	1.72×10^4	4.41×10^5	2.09×10^7	
	1.71×10^3	1.70×10^4	4.25×10^5	1.93×10^8	

(*) In each rectangle upper number is obtained by method of Section 2.4, equation (23).

TABLE 4.2

Mean extinction times computed by the method of Section 4.3, $\mu = .1, x = x_E$.

N \ λ	.105	.110	.115
10^3	1.04×10^3	9.38×10^3	5.12×10^5
10^4	1.41×10^7	3.61×10^{20}	3.86×10^{41}
10^5	2.39×10^{53}	8.90×10^{191}	(*)

(*) Too large to be computed.

TABLE 4.3

	N = 100		200		300		400		500	
λ=.12	16.7	9.13	33.3	12.91	50.0	15.8	66.7	18.3	83.3	20.4
	14.3	8.13	28.3	13.2	44.0	16.8	60.5	19.5	77.4	21.6
	1.17	1.12	1.18	.978	1.14	.941	1.10	.936	1.08	.944
λ=.15	33.3	8.16	66.7	11.5	100	14.1	133	16.3	167	18.3
	30.9	8.73	64.5	11.9	97.9	14.4	131	16.5	165	18.4
	1.08	.934	1.03	.970	1.02	.982	1.02	.990	1.01	.992
λ=.2	50.0	7.07	100	10	150	12.2	200	14.1	250	15.8
	48.9	7.23	99.0	10.1	149	12.3	199	14.2	249	15.9
	1.02	.978	1.01	.990	1.01	.996	1.01	.996	1.00	.994

In left half of rectangle upper number = μ_N, middle number = μ_Q and lower number = $\eta_N = \frac{\mu_N}{\mu_Q}$

In right half of rectangle upper number = σ_N, middle number = σ_Q and lower number = $\zeta_N = \frac{\sigma_N}{\sigma_Q}$

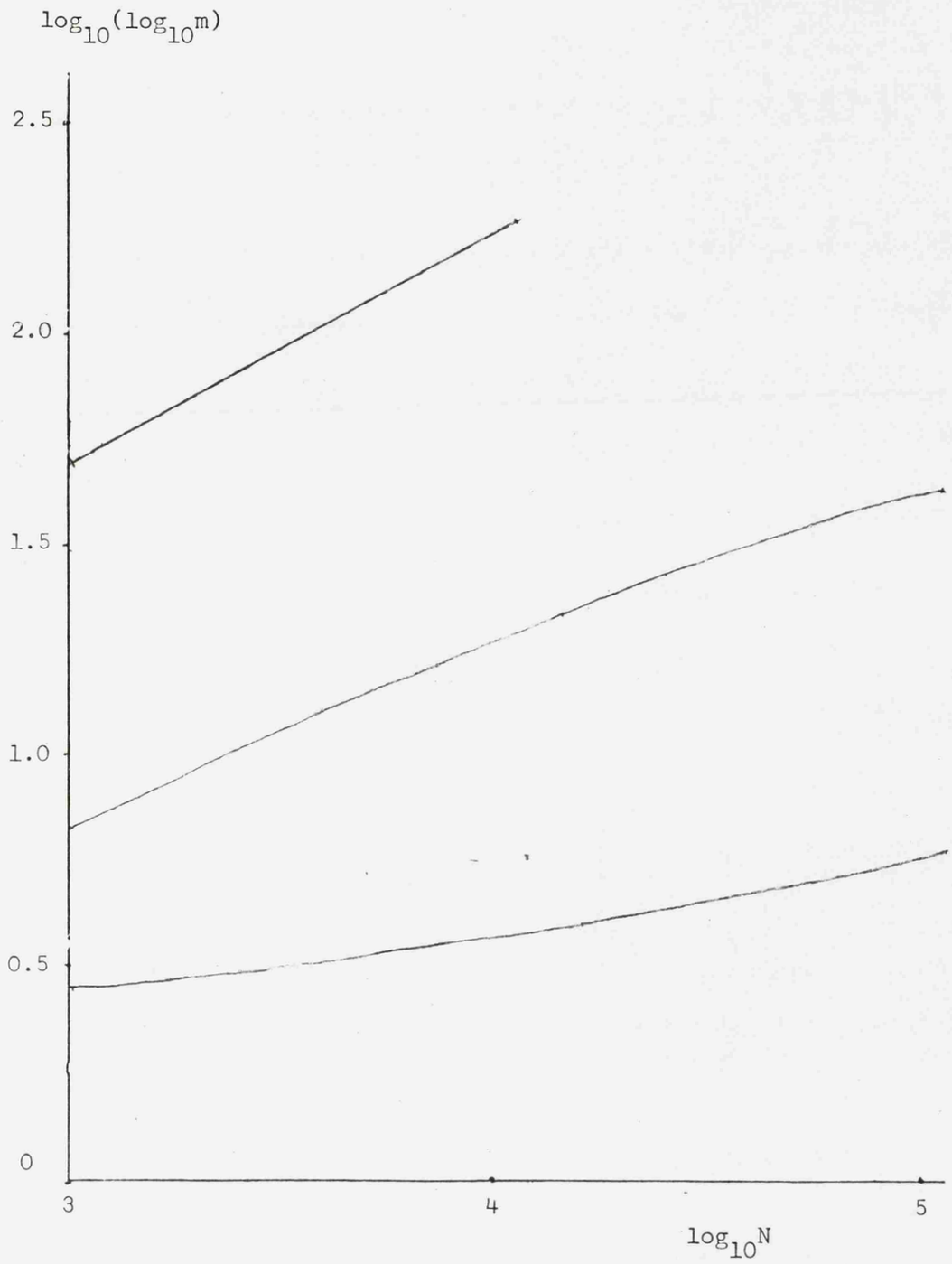
TABLE 4.4

Shows values of L and $\frac{1}{\tau}$ in the linear relationship $\nu = L - \frac{t}{\tau}$

In each rectangle first number is L and second number is $\frac{1}{\tau}$

N \ λ	.105	.110	.115
10^3	3.86 9.62×10^{-4}	4.51 1.07×10^{-4}	4.87 1.95×10^{-6}
10^4	6.17 7.09×10^{-8}	6.81 2.77×10^{-21}	7.17 2.59×10^{-42}
10^5	8.47 4.18×10^{-54}	9.12 1.12×10^{-192}	—

Fig. 4.1



CHAPTER 5

THE SL PROCESS WITH TIME AND AGE DEPENDENT PARAMETERS

5.1 GENERAL COMMENTS

Having developed the SL model so far the aim now is to seek to modify it by incorporating time and/or age dependent birth and death functions so as to achieve greater reality. In fact, in the next chapter a particular isolated breeding community will be considered in this way. This chapter, in which both the theory and the related simulation techniques are developed further, can therefore be regarded as a preliminary to the final aim of showing the relevance of the SL model, at least in its more general form, to actual ecological situations.

5.2 THE SIMPLE BIRTH - DEATH PROCESS WITH TIME DEPENDENT PARAMETERS

In this model, if the birth and death parameters are $\lambda(t)$ and $\mu(t)$ respectively, i.e. are time but not age dependent, then for a population level j, the birth and death rates are simply $\lambda(t)j$ and $\mu(t)j$ respectively. This model has been considered in some detail by KENDALL (1948) who, in particular, showed that a necessary and sufficient condition for extinction to occur with probability 1 is that the integral

$$\int_0^\infty \mu(u)e^{\rho(u)}\,du \qquad (1)$$

should be divergent, where

$$\rho(t) = \int_0^t [\mu(u) - \lambda(u)]\, du \qquad (2)$$

Thus if $\lambda(t) = b(1 + a\sin\omega t)$, $(0 < a \leqslant 1)$, which is an obvious way in which to describe the seasonal breeding pattern of many species, and if $\mu(t) = \mu$, independent of t, then extinction will occur with probability 1 if and only if $b \leqslant \mu$. It is notewothy that this result does not depend on ω.(*)

It is also shown that if extinction is certain then the PDF of T_i, the time to extinction from an initial state i, is

$$\frac{i\mu(t)\, e^{\rho(t)}\left[\int_0^t \mu(u)e^{\rho(u)}\, du\right]^{i-1}}{\left[1 + \int_0^t \mu(u)e^{\rho(u)}\, du\right]^{i+1}} \qquad (3)$$

which for the particular birth and death functions considered here reduces to

$$\frac{i\mu^i C(t)D(t)\left[\int_0^t C(u)D(u)du\right]^{i-1}}{\left[1 + \mu \int_0^t C(u)D(u)du\right]^{i+1}} \qquad (4)$$

where $C(t) = e^{(\mu-b)t}$ and $D(t) = \exp\left[-2ab\omega^{-1}\sin^2(\omega t/2)\right]$. Thus the effect of the periodic content of $\lambda(t)$ on $\tau_i = E(T_i)$ depends essentially on the parameter ab/ω. It can also be seen that as $\omega \to 0$ then the usual results for the case where λ and μ are constant are recovered.

(*) For some ecological situations it would, of course, be more appropriate to take $\mu(t)$ as $d(1 + a'\sin\omega t)$ rather than as a constant. In that case simple calculations will readily show from KENDALL'S result that extinction will occur with probability 1 if and only if $d \geqslant b$.

5.3 THE SL PROCESS WITH t - DEPENDENT BUT AGE INDEPENDENT BIRTH AND DEATH PARAMETERS.

The process (SLT) is defined as previously on the state space $S_N = \{j: 0 \leqslant j \leqslant N\}$ with birth and death rates

$$b_j(t) = \lambda(t)j(1 - \frac{j}{N}) \text{ and } d_j(t) = \mu(t)j \qquad (1)$$

respectively. Also it is assumed that there are positive constants λ_B, μ_A and μ_B such that for all t, $\mu_A \leqslant \mu(t) \leqslant \mu_B$ and $0 \leqslant \lambda(t) \leqslant \lambda_B$.

If therefore the process enters state j at time t, then the waiting time, W(j,t), to the next event, i.e. a birth or a death, has distribution function, $L(w|t,j)$ defined by

$$L(w|t,j) = 1 - \exp\left[-\int_0^w g_j(u + t)du\right] \quad (j \geqslant 1) \qquad (2)$$

where $g_j(t) = b_j(t) + d_j(t)$. The next event is thus a birth with probability

$$p_j(t + w) = \frac{b_j(t + w)}{b_j(t + w) + d_j(t + w)} \qquad (3)$$

where w now is the realised value of W(j,t), and a death with probability $q_j(t + w) = 1 - p_j(t + w)$. Thus we have a non-stationary MARKOV process for which it will be shown that extinction occurs with probability 1, as is the case in the t - independent parameter situation.

Consider first therefore the MARKOV chain M defined on S_N with the following one - step transition probabilities;

$p_{j,j+1} = P_j$, $p_{j,j-1} = Q_j$ for $0 < j < N$, $p_{00} = 1$, $p_{NN} = 0$, $p_{N,N-1} = 1$

and otherwise $p_{ij} = 0$, where $P_j = \underset{t}{\text{Max}}\ p_j(t)$ and $Q_j = \underset{t}{\text{Min}}\ q_j(t) = 1 - P_j$,

since $p_j(t) + q_j(t) = 1$ for all t.

Following therefore the terminology and methodology of CHUNG (1967), Chapter 1, it is clear that in **M** all states apart from 0 are inessential and hence non - recurrent. The state 0 is recurrent. Thus if M_i is the number of steps taken by the process **M** from state i to state 0 then

$$\lim_{n\to\infty} P(M_i > n) = 0 \tag{4}$$

The following lemma will then show that the same result must be true for the SLT process.

Lemma 5.1

If $M_i'(t)$ is the number of steps taken by the SLT process from a state i, entered into at time t, to the state 0, then

$$P(M_i'(t) > n) \leqslant P(M_i > n) \tag{5}$$

for all $t \geqslant 0$, all i such that $1 \leqslant i \leqslant N$ and for all integers $n \geqslant 1$.

Proof

The proof is by induction on n, in which (5) is taken as an inductive hypothesis, H_n say, for some n, for all $t \geqslant 0$ and all i such that $1 \leqslant i \leqslant N$.

Then clearly H_1 is true, for if $\ell(w\,|t,j)$ is the PDF corresponding to the DF $L(w|t,j)$ defined by (2), then for all t

$$P\left[M_1'(t) > 1\right] = \int_0^\infty \ell(w|t,1)p_1(t + w)dw$$

$$\leqslant P_1\int_0^\infty \ell(w|t,1)dw = P_1 = P(M_1 > 1) \tag{6}$$

Also for all t and all i, $2 \leqslant i \leqslant N$,

$$P\left[M_i'(t) > 1\right] = P(M_i > 1) = 1 \tag{7}$$

and (6) and (7) together imply H_1.

Further, for $1 \leqslant i \leqslant N - 1$ we have

$$P\left[M_i'(t) > n + 1\right] = \int_0^\infty \ell(w|t,i)p_i(t + w)\, P\left[M_{i+1}'(t + w) > n\right] dw$$

$$+ \int_0^\infty \ell(w|t,i)q_i(t + w)\, P\left[M_{i-1}'(t + w) > n\right] dw \qquad (8)$$

Thus on the basis of H_n

$$P\left[M_i'(t) > n + 1\right] \leqslant a_i(t)P\left[M_{i+1} > n\right] + b_i(t)P\left[M_{i-1} > n\right] \qquad (9)$$

where $$a_i(t) = \int_0^\infty \ell(w|t,i)p_i(t + w)dw$$

and $$b_i(t) = \int_0^\infty \ell(w|t,i)q_i(t + w)dw$$

Thus as $$p_i(t + w) = P_i - \varepsilon_i(t + w)$$

and $$q_i(t + w) = Q_i + \varepsilon_i(t + w)$$

where $\varepsilon_i(t + w) \geqslant 0$ for all t and w, then

$$a_i(t) = P_i - \delta_i(t) \quad \text{and} \quad b_i(t) = Q_i + \delta_i(t)$$

where $$\delta_i(t) = \int_0^\infty \varepsilon_i(t + w)dw$$

is a non - negative function of t. Thus (9) can now be written as

$$P\left[M_i'(t) > n + 1\right] \leqslant P_i.P\left[M_{i+1} > n\right] + Q_i.P\left[M_{i-1} > n\right] + R_i(t) \qquad (10)$$

where $R_i(t) = \delta_i(t)\left\{P\left[M_{i-1} > n\right] - P\left[M_{i+1} > n\right]\right\}$.

Now in the process M,

$$P(M_{i+1} \leqslant n) = \sum_{j=2}^{n-1} f_{i+1,i-1}^{(j)}\, P\left[M_{i-1} \leqslant n - j\right] \qquad (11)$$

where $f_{i+1,i-1}^{(j)}$ is the probability that the state i - 1 is reached for the first time in exactly j steps from state i + 1.

But clearly $P(M_i \leqslant n)$ is a monotonically increasing function of n for

$$P(M_i \leqslant n+1) = P(M_i \leqslant n) + P(M_i = n+1) \geqslant P(M_i \leqslant n)$$

and so from (11)

$$P(M_{i+1} \leqslant n) \leqslant P(M_{i-1} \leqslant n-2) \sum_{j=2}^{n-1} f^{(j)}_{i+1,i-1}$$

$$\leqslant P(M_{i-1} \leqslant n) \sum_{j=2}^{\infty} f^{(j)}_{i+1,i-1}$$

$$= P(M_{i-1} \leqslant n) \qquad (12)$$

Thus $$P(M_{i+1} \geqslant n) \geqslant P(M_{i-1} > n) \qquad (13)$$

and this implies that $R_i(t) \leqslant 0$ for all t, since $\delta_i(t) \geqslant 0$ for all t. Hence from (10) it follows that for all t

$$P\left[M_i'(t) > n+1\right] \leqslant P_i.P\left[M_{i+1} > n\right] + Q_i.P\left[M_{i-1} > n\right] \qquad (14)$$

i.e. that $$P\left[M_i'(t) > n+1\right] \leqslant P\left[M_i > n+1\right]. \qquad (15)$$

The special case where i = N may be dealt with similarly. Here equation (8) is modified to

$$P\left[M_N'(t) > n+1\right] = \int_0^{\infty} \ell(w|t,N)\, P\left[M_{N-1}'(t+w) > n\right] dw \qquad (16)$$

which again on the basis of H_n leads to

$$P\left[M_N'(t) > n+1\right] \leqslant P\left[M_{N-1} > n\right] = P\left[M_N > n+1\right]. \qquad (17)$$

Thus it has been shown that H_n implies H_{n+1} and so the proof by induction is now complete.

Corollary

An immediate consequence of (4) and Lemma 5.1 is that for all t and all i, $1 \leqslant i \leqslant N$,

$$\lim_{n\to\infty} P\left[M_i'(t) > n\right] = 0 \ . \tag{18}$$

In order now to prove that extinction in the SLT process will occur with probability 1, the following additional lemmas will be required.

Lemma 5.2

If in the SLT process there is a positive constant μ_A such that for all t, $\mu(t) \geqslant \mu_A$, then for all t and all j such that $1 \leqslant j \leqslant N$,

$$\lim_{w\to\infty} P\left[W(j,t) > w\right] = 0.$$

Proof

By definition, from (2), for all t and all j such that $1 \leqslant j \leqslant N$,

$$P\left[W(j,t) > w\right] = \exp\left[-\int_0^w g_j(u + t)du\right]$$

$$< \exp\left[-\mu_A w\right]$$

by the conditions of the lemma, and clearly this tends to zero as w tends to infinity.

Lemma 5.3

If $W_M(k)$ is the maximum of any k consecutive waiting times in the SLT process, then for all $k \geqslant 1$

$$\lim_{t\to\infty} P\left[W_M(k) > t\right] = 0$$

This follows at once from Lemma 5.2 and the standard theory.

The main result can now easily be established

Theorem 5.1

In the SLT process, if $p_{i0}(t)$ is the probability that the process will be in state 0 at time t, for an initial state i, $1 \leqslant i \leqslant N$, then

$$\lim_{t\to\infty} p_{i0}(t) = 1 .$$

Proof

If the process reaches state 0 at time T_i having taken M_i' steps from the initial state i, then for any $n \geqslant 1$

$$P(T_i > t) = P(T_i > t|M_i' \leqslant n)P(M_i' \leqslant n) + P(T_i > t|M_i' > n)P(M_i' > n)$$

$$\leqslant P(T_i > t|M_i' < n) + P(M_i' > n), \qquad (20)$$

since necessarily $P(M_i' \leqslant n) \leqslant 1$ and $P(T_i > t|M_i' > n) \leqslant 1$.

But if $W_M'(n)$ is the maximum of the M_i' waiting times taken by the process in passing from state i to state 0, conditioned on $M_i' \leqslant n$, then

$$P(T_i > t|M_i' \leqslant n) \leqslant P(W_M'(n) > t/n)$$

which tends to 0 as t tends to infinity, by Lemma 5.3.

Hence from (20), we must now have

$$\lim_{t\to\infty} P(T_i > t) \leqslant P(M_i' > n)$$

and so by Lemma 5.1

$$\lim_{t\to\infty} P(T_i > t) = 0.$$

5.4 SIMULATION OF THE SLT PROCESS

The methods of Sections 2.4,2.5 and 2.7 by which it was possible to obtain the moments of T_i, the time to extinction from an initial state i, require that the birth and death parameters are constant. They cannot therefore be applied to the SLT process. Nor does there appear to be any other possible analytic method for dealing with this problem, the solution of which would, in particular, provide the form of the PGF,$G_i(z,t)$, i.e. the PGF of the distribution of states j at time t for an initial state i, along the boundary z = 0 in the z - t plane. This in turn precludes the use of the numerical integration method of Section 3.3 as applied to equation 2.1(9) which is the partial differential equation (*) which governs the developement of $G_i(z,t)$ over the z - t plane. In any case, for the reasons stated earlier, the method is of very limited value. Also the application of the LAPLACE Transform method of BELLMAN et al. to the system of equations 2.2(10), which would now have time dependent coeffecients, would involve severe theoretical and numerical difficulties.

It appears therefore that simulation is the only feasible method by which numerical results can be obtained. In this context consideration will be given specifically to a birth function of the form

$$\lambda(t) = b(1 + a\sin\omega t), \quad (0 \leqslant a \leqslant 1) \tag{1}$$

since this is an obvious way of describing, at least approximately, the seasonal breeding pattern which is a characteristic of many species. In order to simplify the discussion at this stage, however, it is

(*) The method of deriving this equation will show that it is valid for the SLT model as well, provided λ is replaced by $\lambda(t)$ and μ by $\mu(t)$.

assumed, as previously, that $\mu(t) = \mu$, a constant.

In the first place it is useful to consider the equivalent deterministic process defined by, $y(0) = i$ and

$$\frac{dy}{dt} = b(1 + a\sin\omega t)y(1 - \frac{y}{N}) - \mu y \qquad (2)$$

where $y = y(t)$ is the process level at time t.

This equation can be integrated numerically without difficulty by a suitable standard routine. Values of the maximum and minimum levels attained by y(t), which must necessarily be a periodic function of t, are shown for various cases in Table 5.6. Evidently the amplitude of y increases as ω decreases. This suggests that in the analogous stochastic situation, i.e. in the SLT process, $E(T_i)$ regarded as a function of ω , $\tau_i(\omega)$ say, will decrease with ω, at least down to some critical value of ω, ω_c say. In fact, it will be shown by simulation that this is the case.

With regard to the simulation of the SLT process, it is clear that the central problem is to find a simple efficient way of generating the waiting times, W(j,t), between events. This can be achieved by observing that, in accordance with the standard theory, the random variable $V = L(W(j,t)|j,t)$ is uniformly distributed on $[0,1]$. Hence for the specific birth and death functions considered here values, w, of W(j,t) can be obtained from the equation

$$\left[bj(1 - \frac{j}{N}) + \mu j\right]w + \frac{ab}{\omega}j(1 - \frac{j}{N})\left[\cos\omega t - \cos\{\omega(t + w)\}\right] + \ell n(1 - v) = 0 \qquad (3)$$

where v is a realised value of V. The solution of (3) can easily be shown to be unique, and can readily be solved using a standard algorithm. Details relating to these matters and also computer time requirements are given in Appendix 2.

With no prior knowledge of the $\tau_i(\omega)$ v ω profile available, apart from what might be suggested by results such as those exhibited in Table 5.6 for the analogous deterministic model, it is difficult to know what values of ω to select at the outset. However it was found to be much more economical in terms of computer time to search with equal intervals of $\zeta = \log_2(2\pi/\omega)$ rather than of ω itself, and that a fairly definite picture of the $\tau_i(\omega)$ v ζ profile could be established using relatively few values of ζ.

Some simulated estimates of $\tau_i(\omega)$ and $\sigma_i(\omega) = \sqrt{\mathrm{Var}(T_i)}$ based on 50 runs per case are given in Tables 5.1 where the parameter values are selected from N = 100; i = 10,20; b = 0.12, 0.13, 0.14 and 0.15; μ = 0.1, a = $\pm$1 and ζ = 1,2,...,11 as appropriate, and a few cases where N = 1000 are also considered. The relatively large number of simulations was found to be necessary in view of the wide dispersion of extintion times, T_i.

Clearly these tables contain a lot of information. Nevertheless the following broad conclusions seem reasonable and where possible have been validated by standard statistical tests applied to this data.

(1) For an arbitrary $\varepsilon > 0$, there are numbers $\zeta_1 = \zeta_1(\varepsilon)$ and $\zeta_2 = \zeta_2(\varepsilon)$, where $\zeta_2 > \zeta_1$, such that for all $\zeta < \zeta_1$ and all $\zeta > \zeta_2$, $|\tau_i'(\zeta) - \tau_i|$ is less than ε, where $\tau_i'(\zeta) \equiv \tau_i(\pi.2^{1-\zeta})$ and $\tau_i = \tau_i(0)$.

(2) Regarded as a function of ζ, $\tau_i'(\zeta)$ attains a minimum, $\tau_{i,C}'$ say, at a unique value of ζ, $\zeta = \zeta_C$, where $\zeta_1 < \zeta_C < \zeta_2$. Also ζ_C does not vary much with the other parameters and indeed for all the cases considered here $6 < \zeta_C < 8$.

(3) The ratio $\eta = \tau_{i,C}/\tau_i$ decreases as b increases. Thus for N = 100, i = 10, μ = 0.1 and α = - 1, η is about 0.1 when b = 0.12 but about 0.002 when b = 0.15. (*)

This shows the very great reduction in $E(T_i)$ which can be effected by the inclusion of a cyclic birth function in the process. Any idea therefore that the larger values of $\lambda(t)$ attained over the life span of the process will necessarily compensate for the smaller values, whatever the value of ω, is clearly untenable.

(4) For $-\infty < \zeta < \zeta_C$, $\tau_i'(\zeta)$ decreases monotonically as ζ approaches ζ_C. As ζ increases beyond ζ_C there may be some oscillatory behaviour in $\tau_i'(\zeta)$ as it approaches its limiting value τ_i.

(5) If $\zeta_1 < \zeta < \zeta_2$ then the effect which the point of the birth cycle at which the process begins has on $\tau_i'(\zeta)$ can be very considerable. Thus for N = 100, i = 20, b = 0.13 and μ = 0.1, the value of $\tau_i'(\zeta)$ for a = 1 and ζ = 11 is about 8 times as great as its value when ζ = 11 and a = - 1. (See Table 5.1(B))

Finally, it is of interest to consider the distribution of the maximum of the state variable j, in each case, both for zero and non - zero a. In fact, these maxima were recorded both in the simulations just described and also in the simulations of the basic SL model as described in Chapter 2. In each case the mean and standard deviation of the realised maxima were computed. Some results are given in Table 5.2 for the value of ζ at which, in Table 5.1(A), $\hat{\tau}_i(\omega)$ is least, and for a = - 1, 0 and 1, and where N = 100, i = 10 and also b = 0.12, 0.13 and 0.14.

(*) However, $\tau_{i,C}$ cannot in any case be less than $\mu^{-1}\sum_{j=1}^{i} j^{-1}$, if $|a| \leq 1$, since in Section 2.4 this was shown to be the result for τ_i when $\lambda = 0$.

These show that the point of the birth cycle at which the process begins greatly influences the range of realised values of the state variable j in the subsequent history of the process. Thus for the case where N = 100, i = 10, b = 0.14 and μ = 0.1, 95% confidence intervals for the maximum of j are 14.2 to 18.1, 44.0 to 48.4 and 70.3 to 71.9 for a = - 1, 0 and +1 respectively.

Note that in this last case a much larger dispersion of states results than when a = 0, even though $\tau_i'(\zeta)$, for the value of ζ considered here, is much less than τ_i. Also the dispersion is much greater than in the equivalent deterministic model (Table 5.6) where in any case extinction does not occur.

Since, therefore, for many, if not most, species a cyclic rather than a constant birth function is more descriptively appropriate, then it would appear that the ecological implications of these results could be considerable.

5.5 THE DETERMINISTIC LOGISTIC PROCESS WITH AN AGE STRUCTURE

Clearly for most biological populations any adequate theoretical analysis must incorporate an age - dependent birth function. However, before attempting to modify the SL model in his way it is useful first to consider the equivalent age - dependent deterministic process.

To begin with the equation governing the developement of the unrestricted (N = ∞) process is standard, e.g. KENDALL (1949). If x is the age variable, $\lambda(x)$ the birth function, and z(x,t) is the population density function with respect to x at time t, and if also b(t) is the

total population birth rate at time t, and if μ is the death rate, assumed constant here , then

$$b(t) = g(t) + \int_0^t \lambda(x)\, e^{-\mu x}\, b(t - x)dx \qquad (1)$$

where $$g(t) = \int_t^\infty \lambda(x)e^{-\mu t}\, z(x - t, 0)\, dx\,. \qquad (2)$$

Note that in equation (1), the first integral represents the contribution to b(t) by those individuals who were alive at t = 0, and have survived to time t, and the second integral represents the contribution to b(t) by those individuals who were born after t = 0.

A formal solution of (1) can be obtained using LAPLACE Transforms. For if $\bar{g}(s)$, $\bar{b}(s)$,... etc., are the LAPLACE Transforms of g(t), b(t), ... etc., and if $\bar{\ell}(s)$ is the LAPLACE Transform of $e^{-\mu t}\lambda(t)$, then it follows at once from (1) that

$$\bar{b}(s) = \bar{g}(s) + \bar{\ell}(s)\bar{b}(s) \qquad (3)$$

by the standard result for convolution integrals. Thus

$$\bar{b}(s) = \frac{\bar{g}(s)}{1 - \bar{\ell}(s)} \qquad (4)$$

Also $$y(t) = \int_0^t e^{-\mu x}\, b(t - x)dx + e^{-\mu t}\int_t^\infty z(x - t, 0)dx \qquad (5)$$

and as $$\int_t^\infty z(x - t, 0)dx = \int_0^\infty z(x,0)dx = y(0),$$

then taking the LAPLACE Transform of (5) will lead to

$$\bar{y}(s) = \frac{\bar{b}(s) + y(0)}{s + \mu}. \qquad (6)$$

Hence combining (4) and (6),

$$\bar{y}(s) = \frac{\bar{g}(s) + y(0)\left[1 - \bar{\ell}(s)\right]}{(s + \mu)\left[1 - \bar{\ell}(s)\right]} \tag{7}$$

A solution for y(t) can therefore be obtained by inverting (7),which for some forms of $\lambda(x)$ can easily be carried out in terms of standard functions. If this is not possible,then a numerical solution for y(t) could be obtained for most other $\lambda(x)$ of interest using the numerical inversion method of BELLMAN et al.

In particular, consider the general gamma type function

$$\lambda(x) = \frac{b\beta(\beta x)^{q-1}}{\Gamma(q)} . e^{-\beta x} \quad (\beta > 0, q > 1) \tag{8}$$

by which some actual birth functions might, by suitable choice of b, β and q, be well approximated. Such a $\lambda(x)$ has a total mass over x of b and satisfies the main requirements that it is a non - negative unimodal function of x such that $\lambda(0) = 0$ and $\lambda(x) \to 0$ as $x \to \infty$.

In this case, it will be found that

$$\bar{\ell}(s) = \frac{b\beta^q}{(s + \beta + \mu)^q} \tag{9}$$

and a consideration of (9) in relation to (7) will then show that $y(t) \to \infty$ as $t \to \infty$ if the function of s

$$D(s) = (s + \beta + \mu)^q - b\beta^q \tag{10}$$

has a real positive root. This can only occur if r, say, $= b^{1/q} > 1$ and $\beta > \beta_c$ where $\beta_c = \mu/(r - 1)$.

Note that β_c decreases not only as b increases, but also as q decreases, which is to be expected in view of the fact that the mean of x with respect to $\lambda(x)$ is bq/β. If $\beta < \beta_c$ then $y(t) \to 0$ as $t \to \infty$, but if $\beta = \beta_c$ then observing that in this case

$$\lim_{s\to 0} \frac{D(s)}{s} = q(\beta + \mu)^{q-1}$$

it follows from (7) that

$$\lim_{t\to\infty} y(t) = \lim_{s\to 0} s\bar{y}(s) = \frac{(\beta + \mu)\bar{g}(0)}{q\mu} \qquad (11)$$

which can easily be evaluated if the initial age distribution $z(x,0)$ is known.

In the restricted process, i.e. in the deterministic logistic process with an age distribution, $\lambda(x)$ is replaced by $(1 - y(t)/N)\lambda(x)$ and so equation (1) is modified to

$$b(t) = \left[1 - \frac{y(t)}{N}\right]\left[g(t) + \int_0^t \ell(y)b(t - y)dy\right] \qquad (12)$$

A formal solution of equation (12) appears to be out of the question. Nevertheless it has been found possible to integrate this equation numerically by a method based on the LAPLACE Transform procedure of BELLMAN et al. (Full details are given in Appendix 7.) Here it has been applied specifically to cases where $\lambda(x)$ is defined by (8) with $q = 2$, and the initial age distribution $z(x,0)$ is of the form $y(0)\alpha^2 xe^{-\alpha x} = A_0(x)$, say. Some results are shown graphically in Figs. 5.1 where $\alpha = 0.1$, $\mu = 0.1$ and b and β are chosen in accordance with the criteria described below.

Evidently no persistent oscillatory behaviour in $y(t)$ occurs. As $t \to \infty$, $y(t)$ approaches some fixed level $y(\infty)$, say, which varies, of course, with the parameters α, b, β, μ and N. The question therefore arises as to whether it is possible to make certain predictions about $y(\infty)$ in terms of these basic parameters. In fact, this appears to be possible by the following argument.

If $y(0) = y(\infty)$ then assuming that $|y(t) - y(\infty)|$ remains small for all t, the LAPLACE Transform of (12) leads approximately to

$$\bar{b}(s) = \xi\left[\bar{g}(s) + \bar{b}(s)\bar{\ell}(s)\right] \tag{13}$$

where $\xi = 1 - y(\infty)/N$. Thus following the argument for the unrestricted process it would be expected that $y(\infty) >, =$ or $< y(0)$ according as $\beta >, =$ or $< \beta_c'$, where $\beta_c' = \mu/(\sqrt{b\xi} - 1)$. Also it would be expected that there is a number $\beta_c'' > \beta_c$, the critical value of β for the unrestricted process, such that $\beta_c'' < \beta_c'$ and such that if $\beta_c'' < \beta < \beta_c'$ then $0 < y(\infty) < y(0)$, but if $\beta < \beta_c''$ then $y(\infty) = 0$.

In fact, these criteria were confirmed by the numerical results obtained, some of which are exhibited in Figs. 5.1, where the selected values of β are $0.8\beta_c''$, $0.5(\beta_c' + \beta_c'')$, β_c'' and $1.1\beta_c'$.

Values of b are chosen on the basis that the value of

$$\int_0^\infty \lambda(x)A_0(x)dx = \frac{2y(0)b\alpha^2\beta^2}{(\alpha + \beta)^3} \tag{14}$$

falls within the range of values of λ considered in the SL model. We then have some basis for comparing results for the age - dependent with the age - independent versions of the model, both in the deterministic and stochastic forms, even though $z(x,t)$ will, in general, differ from $A_0(x)$ for $t > 0$.

The effect of varying α is shown in Fig. 5.2, and in view of the fact that the mean of x with respect to $A_0(x)$ is $2y(0)/\alpha$, is in agreement with what one would expect intuitively. Evidently there is a critical value of α, α_c, such that for $\alpha = \alpha_c$, $y(t)$ is equal to, or at least very nearly equal to, $y(\infty)$ throughout the time developement of the process. For $\alpha < \alpha_c$, $y(t)$ drops from $y(0)$ to an absolute

minimum, y_{MIN}, before increasing towards $y(\infty)$, (There may be other local maxima and minima.) Also y_{MIN} increases with α, but the value of t at which it occurs is a decreasing function of α. Similar remarks apply to the global maximum attained by y(t) when $\alpha > \alpha_c$.

5.6 THE TIME - AGE DEPENDENT SL PROCESS

In this more general form (SLTA) of the SL process, the birth and death parameters, which may be functions of x and t, are specified as $\lambda(x,t)$ and $\mu(x,t)$ respectively, and as in the previous section $z(x,t)$ is the age density function at time t.

If therefore state j is entered at time t so that $j = \int_0^\infty z(x,t)dx$, then $W_j \equiv W_j(z(x,t),t)$, the waiting time to the next event, has DF L_j given by

$$L_j = L_j(w|z(x,t),t) = 1 - \exp\left[-\int_0^w h_j(u|z(x,t),t)du \right] \qquad (1)$$

where $$h_j(u|z(x,t),t) = \int_0^\infty g_j(x + u, t + u)z(x,t)dx$$

and $$g_j(x,t) = \lambda(x,t)(1 - \tfrac{j}{N}) + \mu(x,t).$$

The fact that the distribution of W_j is conditioned by z(x,t) which in turn presupposes a knowledge of events prior to time t, shows the essentially non - Markov character of the process.

If the next event occurs at time t + w, then it will be a birth with probability

$$p_j = \frac{b_j}{b_j + d_j} \qquad (2)$$

where $$b_j = (1 - \frac{j}{N})\int_0^\infty \lambda(x + w, t + w)z(x,t)dx \qquad (3)$$

and $$d_j = \int_0^\infty \mu(x + w, t + w)z(x,t)dx \qquad (4)$$

and a death with probability $1 - p_j$.

Further if the next event is a death then this will occur in the age interval (x_1, x_2) with probability $D(x_1,x_2)/D(0,\infty)$, where

$$D(a,b) = \int_a^b \mu(x + w, t + w)z(x,t)dx. \qquad (5)$$

It is then possible to show that extinction will occur in the SLTA process with probability 1 in much the same way as in Section 5.3 for the SLT process. Only very minor modifications of Lemma 5.1 are necessary. For Lemma 5.2, $\mu_A > 0$, must now be such that $\mu(x,t) \geqslant \mu_A$ for all x and t. We can then write that for all t and all j, $1 \leqslant j \leqslant N$

$$P(W_j > w) = \exp\left[-\int_0^w h_j(u|z(x,t),t)du\right] \qquad (7)$$

$$< \exp(-\mu_A w)$$

which again tends to zero as w tends to infinity.

The main result, Theorem 5.1, would then be proved as before.

5.7 SIMULATION OF THE SLA AND SLTA PROCESSES.

Having established that for the SLTA process, extinction will occur with probability 1, then it is now the aim to simulate the process so as to get some idea of the way in which mean extinction

times etc., vary with the basic parameters.

In general a difficulty will arise by virtue of the fact that the age variable in reality is necessarily continuous, whereas a purely numerical model must work with age groupings. Thus an estimate must be made of the number of individuals who pass into their next age group during the waiting period between events. This is simple if it is assumed that the distribution of ages within an age group is uniform. However, this in turn requires that the class width be small, and thus that the number of classes is large. For this and other reasons, a satisfactory simulation of the process must necessarily make big demands on computer time.

A further difficulty can arise by virtue of the fact that when the state variable j is small the waiting time between events may be comparable to, or even greater than, the age class interval width h, with consequent distortion of the process In this situation therefore it is necessary to push the process forward by preassigned time intervals which are sufficiently small compared to h. At the end of each such interval, then in accordance with the appropriate probability distribution, a birth or death or no event will occur.

The problem of generating the waiting times $W_j(z(x,t),t)$ with DF defined by 5.6(1) is greatly simplified if $\lambda(x,t)$ and $\mu(x,t)$ take the form $\theta(x)\phi(t)$. In this case the method is essentially that for the SLT process as described in Section 5.4, and is described further in Appendix 3 along with other details of the scheme of simulation.

We begin however by considering the stochastic analogue of the deterministic model of Section 5.5. This is a special case of the general stochastic logistic process, described here as the SLA process, in which the birth/death funtions are x but not t dependent. In fact here the birth funtion $\lambda(x)=b\beta^2xe^{-\beta x}$ is considered together with an

assumed constant death parameter μ. Again the initial age distribution takes the form $A_0(x) = A\alpha^2 x e^{-\alpha x}$, though here $\alpha = 0.1$ throughout. Some results are shown in Table 5.3 where, as in Figs. 5.1, values of β are taken in terms of the critical value β_c', even though whatever the value of β extinction will occur with probability 1. As expected the mean extinction time increases with β. This could be inferred not only from the results shown in Figs. 5.1, but also by arguing that as β decreases individuals must live longer before they reach the age at which they are most likely to reproduce themselves, and thus the probability of their dying before reaching this age is correspondingly greater.

If the age distribution does not depart much from its initial form $A_0(x)$, at least through most of the life span of the process, then a rough order of magnitude comparison can be made between the results here and those of Chapter 2 for the SL process. For example, if $y(0) = 10$, $N = 100$, $b = 7$ and $\beta = 0.9\beta_c$ then, with reference to Table 5.3, the simulated estimates of τ_i and σ_i, the mean and standard deviation of the time to extinction from an initial state i, are $\hat{\tau}_{10} = 271$ and $\hat{\sigma}_{10} = 196$. On the other hand, the value of the expression 5.5(14) here is 0.121 and for SL(.12, .1, 10, 100) $\tau_{10} = 370$ and $\sigma_{10} = 370$. Other comparisons can be made similarly, and as a general conclusion it appears that the reduction in τ_i effected by the presence of an age distribution increases with τ_i.

Finally consider the SLTA process with birth function

$$\lambda(x,t) = b\beta^2 x e^{-\beta x}(1+a\sin\omega t)$$

which incorporates both an age structure and a cyclic effect, and $\mu(x,t) = \mu$, a constant, (= 0.1).

The computer time required to simulate such a model was found to be considerable and thus only a relatively few cases could be considered considered. These are defined by b = 4 and 5, $\beta = \beta_c'$, ζ = 3, 4, ..., 9, N = 100 and i = 10 with an initial age distribution $A_o^*(x) = A\alpha^2 x e^{-\alpha x}$, where α = 0.1. The results are shown in Table 5.4 and comfirm the main trends of Table 5.1 for the SLT process. Also it appears here that the critical value of ζ, namely ζ_c, as defined in Section 5.4, is about 6 for both value of b.

Also the results of Table 5.5 show again that the presence of a cyclic birth function can greatly increase the variation of the state variable j over the life span of the process, particularly when ζ is in the neighbourhood of $1.5\zeta_c$.

TABLE 5.1(A)

Simulated values of $\hat{\tau}_i(\omega)$ and $\hat{\sigma}_i(\omega)$ for the SLT process where $\lambda(t) = b\{1 + a\sin(\omega t)\}$ and $\mu(t) = .1$, all t, i = 10, N = 100.

Notes to these results will be found on the next page.

		b a = - 1.0				b a = 1.0			
		.12	.13	.14	.15	.12	.13	.14	.15
ζ	0	248 289	1260 1453	4450 5860		332 391	1025 1100		
	1	372 386	972 937	4900 5470		395 414	1017 925		
	2	294 305	1170 1140	4330 3880		522 544	953 948		
	3	330 338	1150 1250	3170 3730		371 350	1110 1220		
ζ	4	348 388	945 1040	2740 2490	14000 16300	402 390	1050 844		
	5	206 201	480 536	2410 2530		313 277	676 672	2650 2430	
	6	142 230	125 159	294 408	453 695	218 136	401 279	588 449	1006 868
	7	45.1 24.9	56.2 49.0	49.5 48.0	47.72 27.96	147 61	154 86.3	158 89.9	175 92.1
ζ	8	48.8 17.7	45.0 11.9	54.0 16.2	60.6 16.5	192 19.6	187 21.7	191 11.2	195 250
	9	64.2 22.5	71.1 24.4	71.5 17.1	75.5 24.4	320 62.6	326 64.1	332 48.3	334 67.1
	10	76.2 30.1	94.0 32.3	97.8 36.3	119 32.5	554 188	609 81.7	572 179	642 24.2
	11	122 41.4	135 57.7	136 59.1	164 60.5				1200 40.9

Notes to Tables 5.1(A),(B) and (C).

The quantity ζ is defined by, $\zeta = \log_2(2\pi/\omega)$.

In each rectangle the upper number = $\hat{\tau}_i(\omega)$ and the lower number = $\hat{\sigma}_i(\omega)$.

Number of simulations per case = 50.

Lack of computer time precluded the completion of Tables 5.1(A) and 5.1(C).

5.1(B)

$i = 20 \quad N = 100$

	a = −1		a = +1	
	b = .12	.13	.12	.13
0	495	914	487	1246
	424	747	432	1069
1	362	905	428	962
	381	947	383	930
2	400	1303	439	1250
	348	1470	337	2220
3	417	1340	529	1050
	368	1040	421	966
4	332	808	431	1110
	322	795	324	1020
5	351	693	348	7310
	271	533	216	721
6	136	292	263	350
	118	294	180	247
7	76.3	70.2	136	145
	80.0	50.7	49.4	57.2
8	59.6	59.1	190	195
	15.7	15.2	12.5	36.3
9	72.6	76.7	332	335
	18.2	17.0	17.9	15.9
10	90.8	99.5	611	616
	29.1	29.2	31.1	25.9
11	120	148	1110	1170
	43.1	43.8	219	40.5

5.1(C)

N = 1000, i = 100, μ = .1, a = ±1

	b	ζ = 6	7	8	9	10
a=-1	.105	620 613	134 108	76.3 14.6	94.3 15.8	124 16.1
	.11	2032 2636	259 274	74.7 11.6		
a=+1	.105	710 448	312 167	211 140	356 16.7	
	.11	1880 1570	417 239	216 37	362 15.9	

TABLE 5.2

Mean and standard deviation of maxima attained in 50 simulations for $\zeta = \zeta_c'$, $\mu = 0.1$, i = 10 and N = 100.

b	a = -1	0	1
.12	13.2 5.86 (7)	25.6 9.69	61.2 7.39 (7)
.13	13.5 3.08 (8)	34.6 13.8	66.1 6.36 (7)
.14	16.2 13.5 (7)	46.2 15.5	71.1 5.66 (7)

In each rectangle, upper number = mean of maxima attained, and second number equals the corresponding standard deviation. In outside columns number in brackets = ζ_c'.

TABLE 5.3

Simulated results for $\hat{\tau}_i$ and $\hat{\sigma}_i$ for the SLA process for various values of k and b where $\beta = k\beta_c'$, $\lambda(x,t) = b\beta^2 xe^{-\beta x}$, $\mu(x,t) = .1$, $N = 100$ and $i = 10$ with an initial age distribution $A\alpha^2 xe^{-\alpha x}$, $(\alpha = .1)$

k \ b	4	5	6	7
.9	86.0 54.5	124 97.8	122 85.5	271 196
1.0	126 112	202 166	242 216	719 746
1.1	226 221	357 351	531 519	
1.2	336 305	904 966	1628 1611	

In each rectangle upper number = $\hat{\tau}_i$

Number of simulations per case = 100.

TABLE 5.4

Simulated results for $\hat{\tau}_i$ and $\hat{\sigma}_i$ for SLTA process for various values of $\zeta = \log_2(2\pi/\omega)$ and b where $\lambda(x,t) = b\beta^2 x e^{-\beta x}\{1 + \sin(\omega t)\}$, $\mu(x,t) = 0.1$, $N = 100$, $i = 10$ with an initial age distribution $A\alpha^2 x e^{-\alpha x}$, $(\alpha = .1)$ and $\beta = \beta_c'$.

b \ ζ	3	4	5	6	7	8	9
4	143	132	106	87.3	104	170	286
	119	104	56.9	39.7	14.7	28.3	86.1
5	183	163	120	94.5	109	172	296
	126	121	73.4	50.3	25.6	28.6	78.9

In each rectangle, upper number = $\hat{\tau}$.

Number of simulations per case = 100.

TABLE 5.5

Mean and standard deviation of maxima attained in 100 simulations of SLTA process for various values of ζ and b as in Table 5.4.

b \ ζ	3	4	5	6	7	8	9	
4	19.6	21.6	26.6	35.1	52.4	61.1	61.0	19.0
	5.61	6.59	7.34	11.1	11.7	10.1	16.8	6.92
5	22.6	22.6	27.8	38.4	53.4	60.4	62.1	21.7
	6.43	6.20	7.57	10.1	9.94	10.2	15.1	7.88

TABLE 5.6

Maximum and minimum values attained by y in the SLT process as defined by equation 5.4(2), where $y(0) = N(1 - \rho)$, $(\rho = \mu/b)$, $N = 100$, $\lambda(t) = b\{1 + a\sin(\omega t)\}$ and $\mu = 0.1$, for various values of b and ω.

$b = .12$, $y(0) = 16.7$, $a = 1.0$.

ω	$\pi/4$	$\pi/32$	$\pi/64$
Max.	20.4	34.8	55.2
Min.	15.6	9.7	< 3.1

$b = .14$, $y(0) = 28.6$, $a = 1.0$.

ω	$\pi/4$	$\pi/32$	$\pi/64$
Max.	35.7	51.0	63.1
Min.	25.0	15.2	< 3.8

FIG. 5.1(A)

y(t) v. t for the age - structured Deterministic Logistic Process of Section 5.5 for various β.

N = 100, α = 0.1, y(0) = 20, $\bar{b}$ = 4 and μ = 0.1

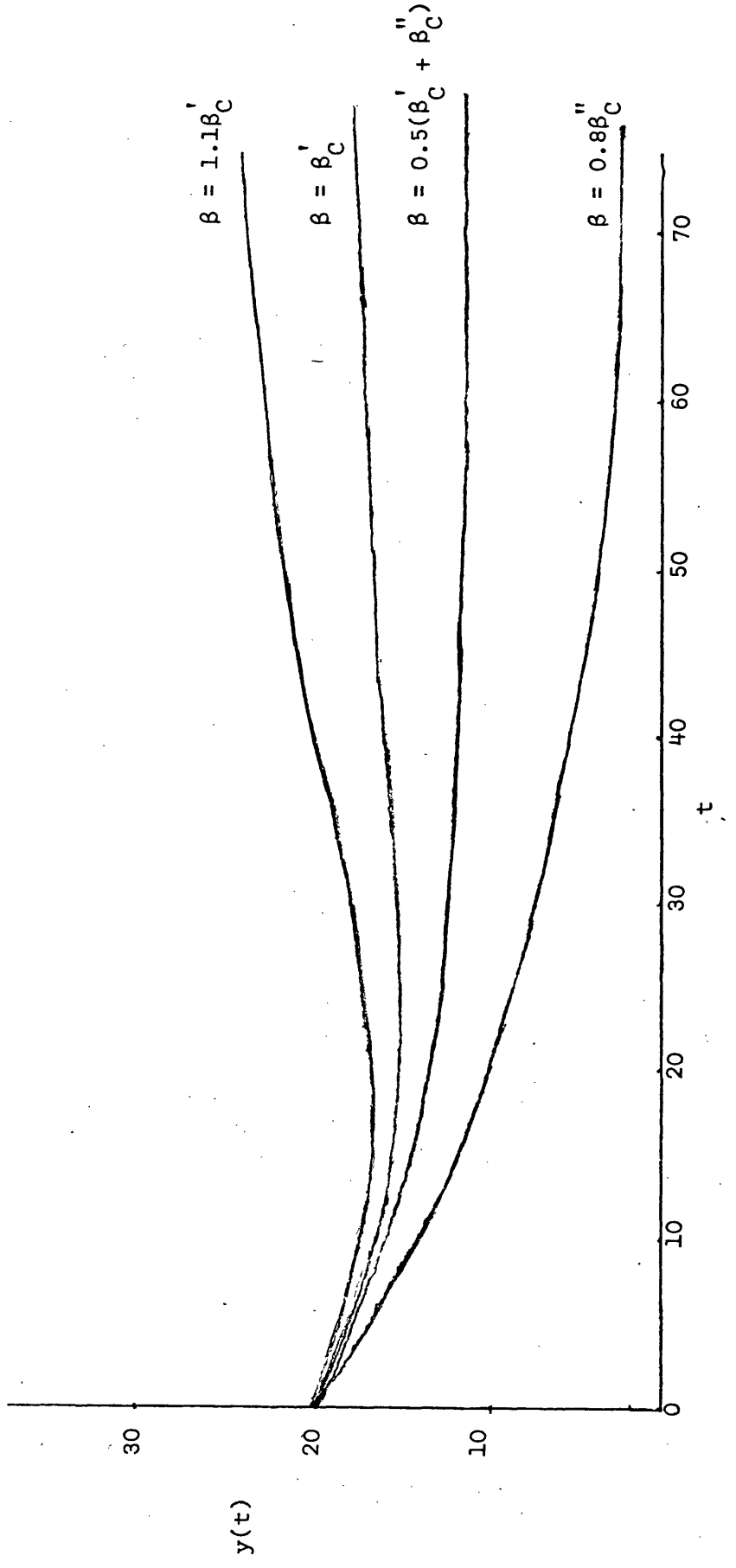


FIG. 5.1(B)

y(t) v. t for the age - structured Deterministic Logistic Process of Section 5.5 for various β.

N = 100, α = 0.1, y(0) = 20, b = 7 and μ = 0.1

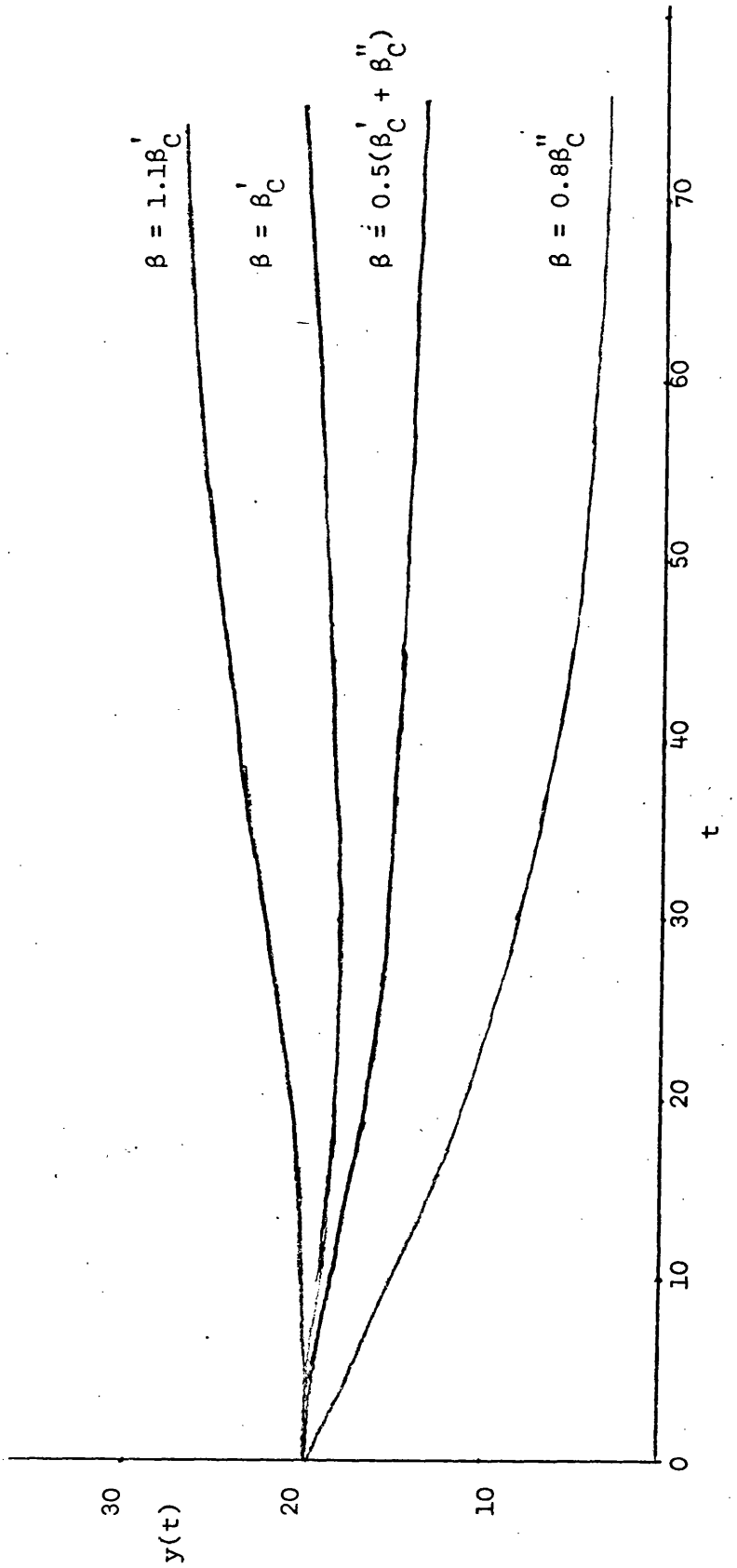


FIG. 5.2(A)

y(t) v. t for the age - structured Deterministic Logistic Process of Section 5.5 for various α.

N = 100, y(0) = 20, β = β_C', b = 4 and μ = 0.1.

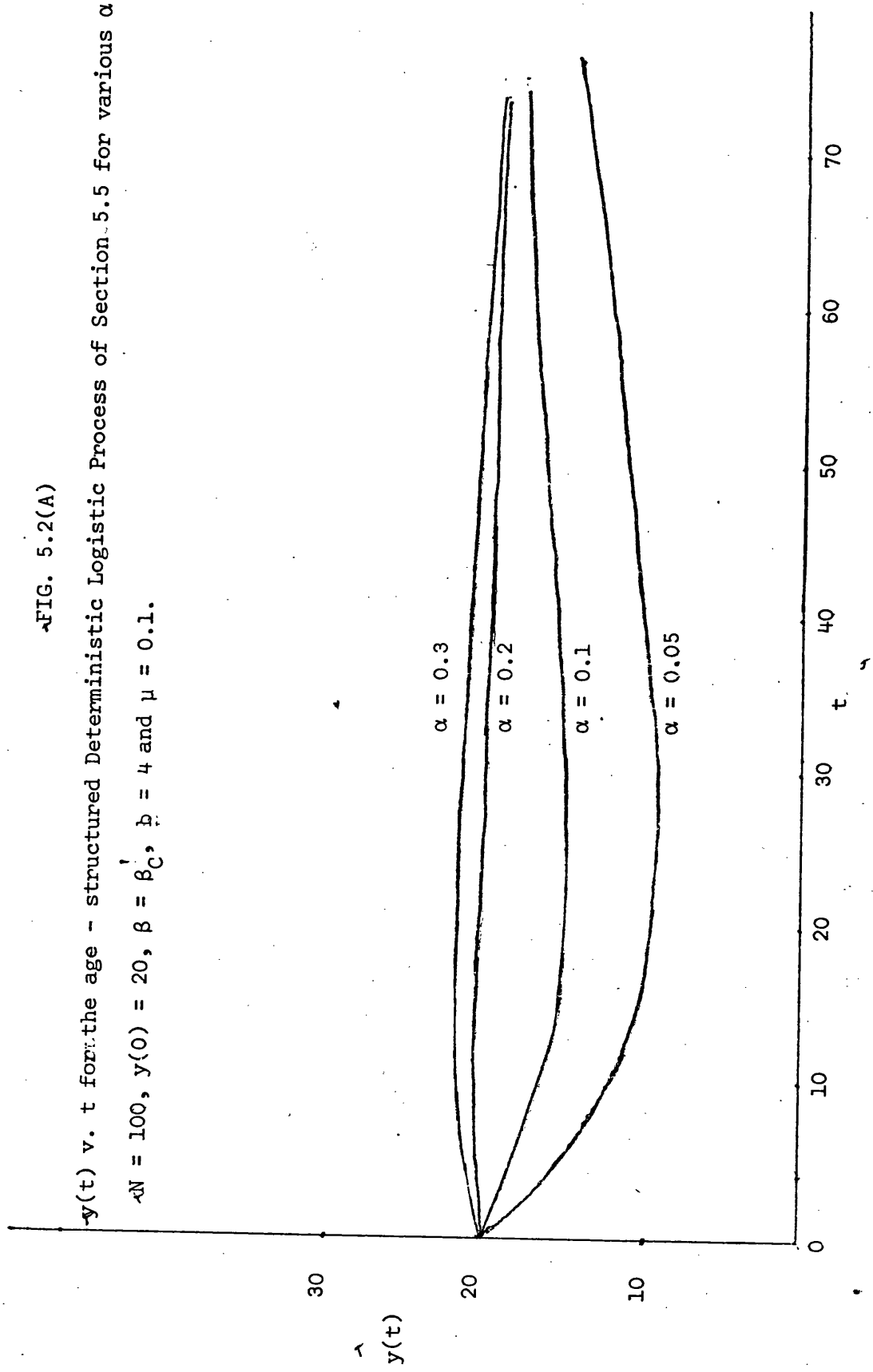
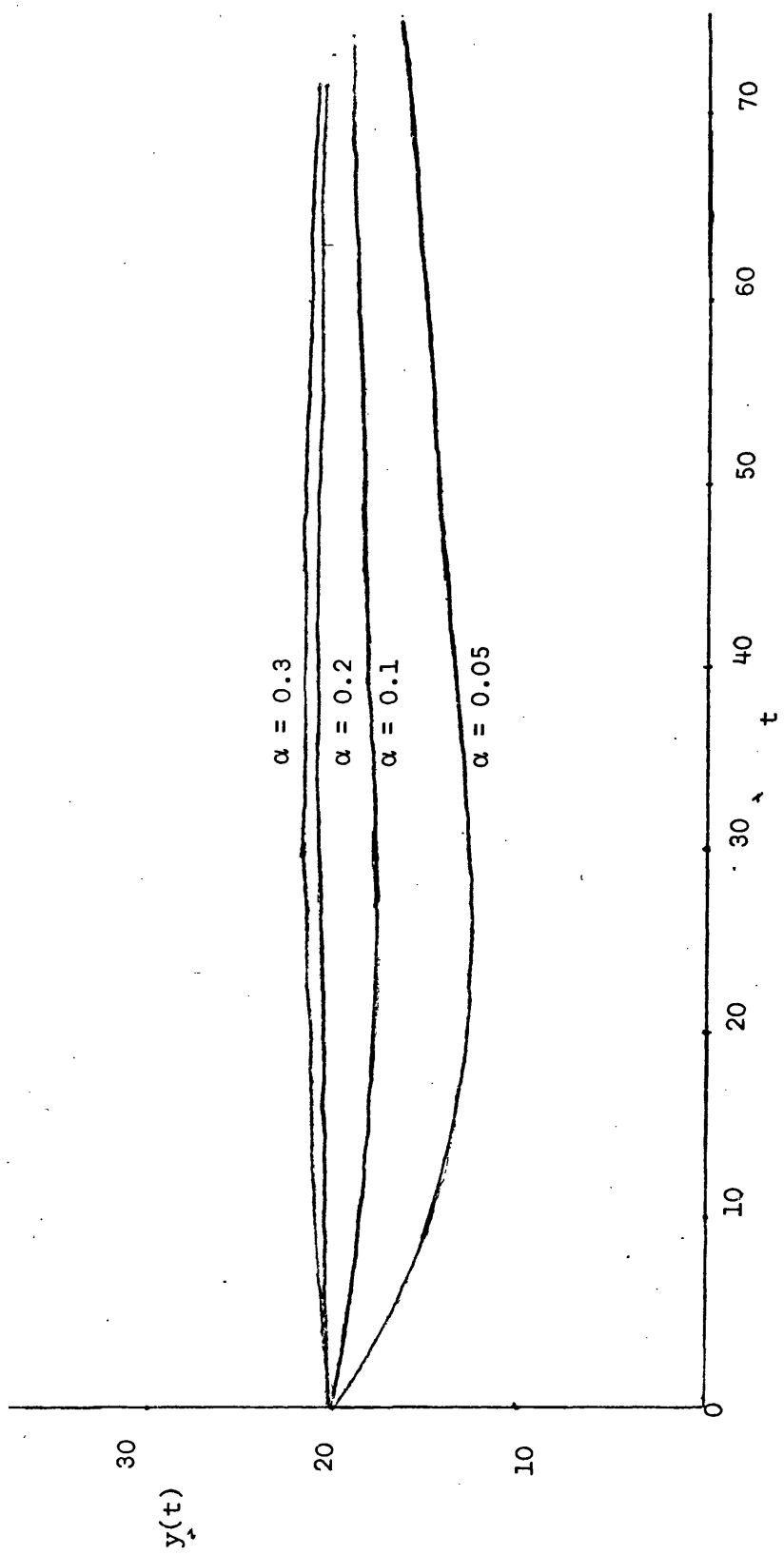


FIG. 5.2(B)

y(t) v. t for the age - structured Deterministic Logistic Process of Section 5.5 for various α.

N = 100, y(0) = 20, β = β'_e, b = 7 and μ = 0.1.



CHAPTER 6

AN ECOLOGICAL EXAMPLE OF THE SL PROCESS WITH MODIFICATIONS

THE SHEEP POPULATIONS OF ST. KILDA WITH SPECIAL REFERENCE TO HIRTA

6.1 GENERAL CONSIDERATIONS

In the previous chapter a number of numerical techniques were developed for dealing with the SL process in its more general form where age and time dependent birth functions are incorporated. They could also be applied, of course, to the still more general and ecologically realistic situation where the death rate is also age and time dependent. A constant death rate was assumed merely to keep the model relatively simple, and to keep the discussion within reasonable bounds.

However, it should especially be emphasised that although simulation appears to be the only way of gaining some insight into the overall behaviour of the general process, nevertheless it is a fundamental theoretical result, as proved in Theorem 5.1, that extinction is inevitable. In fact, the class of age and time dependent rates for which this central conclusion is valid is very wide, and would appear to include any possible actual ecological situations of interest, and certainly the one that will be considered in this chapter.

This in turn raises a fundamental question. Are all closed communities at risk in this way therefore, and thus are immigration and emigration patterns essential survival mechanisms even when no special adverse environmental factors are present? Qualitatively the analysis carried out so far would imply an affirmative answer to

this question. Nevertheless although this conclusion is perhaps an important factor in the understanding of species survival problems, its value is clearly greatly enhanced if also some indication of its quantative implications for particular cases can be obtained. It is the aim of this chapter to show how this might be achieved.

In simple terms therefore an ecological problem of interest for which this analysis might provide an answer is this. Given an isolated breeding community for which the environmental factors are known, at least in the main, what, in the absence of catastrophes, is its expected life span? Of course, it is possible to extend the methodology developed so far to include immigration and emmigration and perhaps show in quantitative terms how these factors can avert or accelerate extinction. This more usual situation would certainly be a worthwhile area of further investigation, but it is quite beyond the scope of this chapter. In any case we would then be dealing with a conceptually different situation.

At the outset therefore we seek an isolated breeding community for which the following information is available:

i) The overall area within which the community is enclosed, and hence its carrying capacity.

ii) The natality pattern and rates.

iii) The age structure of the population over a period of time. From this it will be possible to determine the mortality rate as a function of age. Additionally, it will be necessary to know the distribution of mortality over the year.

iv) Other factors such as the variation of the per-capita nutritional energy with population density and with time of year.

v) Reliable records of the population level over a sufficiently long period of time. This is essential if the model is to be validated.

One such community for which all the above information is available is the present flock of Soay sheep on Hirta. This island is one of the St. Kilda group situated in the Atlantic about 80 km. due west of Harris in the Outer Hebrides. There is an extensive literature on St. Kilda generally, and much important field work has been carried out on Hirta, in particular. Studies which are of particular relevance here are BOYD, (1953), (1964) and (1974), BOYD et al, (1964), GRUBB (1974), GRUBB and JEWELL (1966) and (1974), GUNN and DONEY (1964), JEWELL (1966), LEVER (1977), MILNER (1974), MILNER and GWYNNE (1974), POORE and ROBERTSON (1949) and WILLIAMSON and BOYD (1960).

An overall account and, in some cases, an extension of some of this work can be found in JEWELL et al. (1974). This summary contains all the essential demographic information required for our purposes here, and much else besides. From this standpoint it must be regarded as the authoritative work on the subject. It will thus be used as a basis for the population model to be described later. First however, a brief account of the historical background of the present sheep population on Hirta will be given.

6.2 HISTORICAL BACKGROUND

There are four islands within St. Kilda, Hirta, Soay, Boreray and Dun with areas of 1573, 243, 190 and 79 acres respectively, and also a large number of stacs. The name Soay is Norse in origin and means literally 'sheep island'. However, there is now no agreement between contemporary investigators as to whether this signifies that sheep were introduced there by the Norsemen or whether there were flocks there already when they arrived. This question cannot be resolved until adequate archealogical evidence is available. Nevertheless, what does appear to be beyond dispute is that a primitive pure breed of sheep has been present in a wild isolated state on Soay for at least a thousand years. Moreover the sheep there have no competitors or predators and by all accounts human interference has been slight, at least until very recently.

Access to Soay is indeed very difficult. It is essentially a plateau bounded by cliffs of over 1000 ft. for the most part. There is no natural harbour. Consequently, although this island stands a little under $\frac{1}{2}$ km. from Hirta it appears that the St. Kildans, i.e. the inhabitants of Hirta*, paid little attention to it. About yearly there were raiding parties from Hirta and a few sheep taken off. By all accounts these were extremely hazardous undertakings. Even some recent scientific, and presumably well equipped, expeditions to St. Kilda have failed to secure more than a very temporary landing there.

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* Since medieval times at least, there have been no human settlements on St. Kilda other than on Hirta.

Thus on account of their almost totally isolated state and of the extreme simplicity of their environment the sheep of Soay have come to be a subject of very considerable interest to ecologists. WILLIAMSON and BOYD (1960) describe them as 'one of the faunal treasures of Britain'.

The origin of the Soay breed and its relationship to other primitive and developed breeds is discussed by ELWES (1912) and EWART (1913 and 1914). Also RYDER (1968) who considers this question more from an evolutionary than a contemporary standpoint, emphasises that although the present Soay sheep of St. Kilda are in a wild state the breed generally was domesticated in earlier times. In fact, he claims them to be the most primitive domestic sheep in Europe. Moreover referring to an earlier (1964) paper of his on the subject he concludes that 'During the whole prehistoric period the main, although not necessarily homogeneous stock was probably small, horned and brown, and the Soay sheep can perhaps be regarded as a survivor of this type.'

In modern sheep farming, however, the Soay breed, despite its obvious survival qualities, is not employed, the more recent breeds being superior for wool and meat. Nevertheless some attempts by naturalists to establish small communities of Soays outside St. Kilda have been at least partially successful, and an interesting account of these is given by LOCKLEY (1960).

The St. Kildans maintained sheep both on Boreray, where mainly if not exclusively, the Scottish blackface breed is to be found, and of course on Hirta itself. Their home flock was thus a mixture of Soays and Blackface and certainly not a pure breed.

There does not appear to be much information in the literature about sheep populations on Dun. MARTIN (1698) implies that there were sheep there in his time, and POORE and ROBERTSON (1948) say that this was so in 1909. However, they also say that there were definitely no sheep on this island after 1930.

Two events have occurred on Hirta this century whose combined effect may prove to be of great importance to ecology. Firstly the St. Kildans finally evacuated Hirta in August 1930 to settle on the mainland, and attempted to take with them all the sheep on that island. A few blackface however evaded the final round up.

Secondly in 1932, the then owner, the Marquis of Bute, who was anxious to establish a nature reserve, transferred 107 sheep (*) from Soay to Hirta. It is this flock, greatly increased in size since the year of its establishment which has been the object of the detailed and painstaking field work referred to earlier, and which will now be the main subject of discussion for the rest of this chapter.

6.3 DEMOGRAPHIC DATA FOR THE PRESENT SHEEP POPULATION OF HIRTA

For the first twenty years of its existence on Hirta the new colony of Soays was not subjected to accurate population counts. Such naturalists who visited the island during that period came mainly to observe the other forms of wild life present there, of

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(*) According to WILLIAMSON and BOYD (1960) the composition of this foundation stock was 20 rams, 44 ewes and 43 lambs.

which the sea-birds are especially numerous, and made only incidental estimates of the sheep population. According to BOYD (1974) these were 500 head in 1939, between 400 and 450 in 1947, and between 650 and 700 in 1948. Clearly these figures do little more than indicate an upward but irregular trend in the population total.

Also BOYD states that the first systematic census was conducted in 1952 and then annually from 1955 and always by the same method and in May or June. His data is exhibited in Table 6.1.(*)

In addition there is an account by GRUBB (1974) of the population dynamics of the subpopulation of sheep of the Village Glen. This is not entirely isolated from the main sheep population of Hirta. A small amount of migration does occur. In particular, GRUBB's data shows the age-sex composition of this subpopulation over a number of years, and he has thus constructed a generalised life-table for both males and females.

In general, on the basis of the various accounts given by field workers, the overall population dynamics of the Soay sheep of Hirta may be summarised as follows:

(i) Lambing occurs almost totally within the month of April and the sex ratio for lambs is very nearly 1:1.

(ii) Effective grazing becomes very limited at the end of December. The sheep therefore starve from the beginning of the year to early April. Their ability to survive thus depends very critically on the energy they were able

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(*) Details of how the census is carried out may be found in BOYD et. al. (1964).

to store during the previous year's grazing, and also of course on the current winter conditions. Thus almost all mortality occurs over the months February to April.

(iii) Population growth is density dependent. As the number of individuals increases then the per capita nutritional energy available must necessarily decrease. The effect of this will mean that at the end of the year fewer individuals will possess sufficient stored energy to survive the crucial period January to April. Moreover ewes who do survive this period may not themselves be able to provide adequate maternal care for their offspring, who are thus in turn adversely affected. The population thus crashes and subsequently begins to recover. It is in this way that the cyclic pattern evident in BOYD's data is maintained.

(iv) The mortality rate for rams is much higher than for ewes. Field workers generally argue that this is due to rams depleting their energy reserves during the rut , which occurs in November. This lost energy is not recovered before January and thus rams are much more susceptible than ewes to the hazards of the winter period. This phenomenon is evident in BOYD's data where the ratio of the number of ewes to the number of rams is never less than 3:1 and for two of the recorded years is as high as 11:1.

6.4 STOCHASTIC MODEL OF THE SHEEP POPULATION OF HIRTA

6.4.1 General Aims of the Model

It should be made clear at the outset that it is not the aim here to model the population in detail in some exact predictive sense. Indeed the stochastic approach essentially precludes such an aim which can only have meaning from the deterministic standpoint, though whether there it is a realistic objective is another matter. Something along these lines, however, does appear to have been a attempted for MILNER (1974) outlines a biomass/energy-flow deterministic analysis of the sheep population of Hirta. Nevertheless he says that the predictive value of his model is not high.

From the stochastic standpoint it may not be necessary to include such detail in order to evaluate fundamental ecosystem quantities such as the mean time to extinction or the probability that the community of interest will not become extinct during a given interval of time. However, in order to establish quantitatively exactly how true this last statement is it would be necessary to construct a probabilistic model of great detail, and this is now possible in view of the mass of information available, and compare results obtained with those of simpler models, and of course with real data.

This would be a major undertaking and is certainly not attempted here. Instead the objective is to fit a possible stochastic model of the logistic type to this particular ecosystem, indicate its limitations, and then modify it so that it more nearly describes the reality to which it is meant to apply.

6.4.2 Extending the SLTA Model of Sections 5.6 and 5.7

The discussion of Section 6.3 showed that sufficient data is available to meet the requirements 6.1(i) to (v), and that therefore it is possible to construct a population model of the SL type for the Soay sheep of Hirta with realistic age and time dependent birth and death functions. Such a model could be simply a version of the SLTA process of Section 5.6. Of course, the birth and death functions would be a good deal more complicated than those employed there, but nevertheless, subject perhaps to a few further minor modifications, the underlying methodology is still applicable.

However, in view of the great variation in the ratio of the number of females to males which ranges from 1:1 at birth to as high as 11:1 ewes to rams in adulthood for some years, it cannot be satisfactory to deal with the population only in terms of its age composition, as previously. The entire age-sex composition must be taken into account.

As in Section 5.7 for the SLTA model, there is again the problem of selecting the appropriate groupings of the age variable x. If these are too large substantial distortion of the process may occur. If on the other hand they are taken so small that discontinuity errors are effectively eliminated the consequent demands on computer time may be excessive. Nevertheless, by reason of the very nature of the natality and mortality data, the obvious choice of unit of time is one month, and initially therefore the model was developed with this period as the age class interval over the entire life span of both sexes. For convenience this is described as the A1 age class specification.

Taking 10 years as the maximum age to which any sheep will live[*] it follows that the A1 specification requires a total of 120 age groups for both males and females. Moreover, since an account of the nature of the seasonal breeding pattern these age distributions are necessarily very broken up then the procedure for transferring the appropriate number of individuals in and out of each group at the end of the (random) interval of time between two consecutive events is necessarily a good deal more complicated than in the case of the SLTA model. This factor together with the large number of age groupings first noted precludes the use of the A1 age-class specification other than for the development stage.

Once this stage has been successfully completed, however, larger age groupings can be considered, at least experimentally. In the end the age class specification A2 was adopted in which each sex has just two age groups, defined by $0 \leqslant x \leqslant 12$ and $12 < x \leqslant 120$. A few comparisons of results obtained from the model with the A1 and A2 specifications showed good agreement, at least for the simulation of the Hirta sheep population. For simulations of the smaller populations on the other islands the comparison was not so satisfactory, but there were no major inconsistencies.

It was therefore considered appropriate to proceed with the A2 specification, and as the computer time needed for each case was thus substantially reduced, a wide range of situations could be considered.

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[*] Exceptionally some ewes do live beyond this age, but their contribution to the population total appears to be negligible.

Of course, before actually carrying out these simulations the details of such matters as the initial age distribution for both sexes, choice of mortality and natality functions and the estimation of N, the carrying capacity have to be worked out. These will now be described, but all other details about the setting up and running of the model will be found in Appendix 4.

6.4.3 The Initial Age Distributions

This is based on GRUBB's data which gives the age distributions for both sexes for the years 1960 to 1967 for the Village Glenn. It is assumed therefore that they are typical of the island as a whole.

In order to make a comparison between simulated and actual results for as long a continuous period of time as possible it was decided to initiate the model with the 1955 total. Since however no age distribution data is available for that year it was thought reasonable to use the 1960 distribution, appropriately scaled, since that was also a year of relatively low population density.

Clearly it would be of interest to ascertain how susceptible the results are to the form of the initial age distribution, but a lot of cases would have to be considered if this was to be determined in any definite quantative way, and in fact this was not attempted here.

6.4.4 The Birth Function

This takes the form

$$\lambda(x,t) = b(1 - \frac{j}{N})\theta_1(x)\phi_1(t)$$

where j is the level at time t, $\theta_1(.)$ and $\phi_1(.)$ are normalised functions and b is a scaling factor to be chosen later in the light of available overall fertility data.

The exact specification of $\theta_1(x)$ is complicated by the fact, as shown by GRUBB, that lambs of yearling ewes have a much poorer survival rate at high densities than at low. Thus there is also an age-selective density dependent aspect of the natality pattern, but it will be supposed here that its effect on the general population development is not great and it will not be represented in the birth function therefore.

In general, the survival rate of lambs increases with the age of dams up to about 3 years, and thereafter remains much the same for older ewes, who in fact are capable of producing off-spring up to the end of their life. Soay sheep do not have a senile phase.

This implies that $\theta_1(x)$ takes the form

$$\theta_1(x) = 0 \text{ for } x \leqslant 12,$$
$$= g(x) \text{ for } 12 \leqslant x \leqslant 36,$$
$$= 1 \text{ for } x \geqslant 36,$$

where $g(x)$ is some suitable monotonic function such that $g(12) = 0$ and $g(36) = 1$

Again computer time limitations preclude the consideration of a wide variety of $g(x)$, but it seems reasonable to conjecture that the results obtained would not be substantially affected by small variations in the form of $g(x)$.

Actually a fundamental parameter here is the mean of x with respect to the age component of the birth function, namely

$$\mu_g = \int_0^\infty xg(x)dx$$

as was shown to be the case, for example, in sections 5.5 and 5.7. A likely result therefore, which can only be conjectured here, is that the model is robust with respect to all biologically sensible functions $g(x)$ which appertain to the same value of μ_g.

The specification of $\phi_1(t)$ is more straightforward. The general form is

$$\phi_1(t) = h(t') \text{ when } 0 \leqslant t' \leqslant 1,$$
$$= 0 \text{ otherwise,}$$

where $h(t')$ is some suitable function on the interval $[0,1]$ of $t' = t - 12\left[\frac{t}{12}\right] - 3$.

Again it is supposed that a detailed form for $h(\cdot)$, as could be established for example on the basis of the results of GRUBB and JEWELL (1974), is unnecessary in terms of the objectives here. Any one of a wide class of normalised, but not necessarily unimodal functions, would probably serve equally well.

In view of these remarks therefore it was decided to take simply

$$h(t) = \tfrac{\pi}{2}\sin(\pi t).$$

The value of b is obtained from

$$\int_0^{12}\int_0^{\infty} \lambda(x,t)A_0(x)dxdt = Bj_{2,0}$$

where $A_0(x)$ is the initial age distribution of those females who will produce offspring at the next lambing period

$$j_{2,0} = \int_0^{\infty} A_0(x)dx$$

is the total number of such females, and B is the average number of surviving lambs per ewe to be expected.

Of course, this is not entirely satisfactory in that the female age distribution could alter substantially by the start of the next lambing period, i.e. April, though simulation showed this not to be the case. Nevertheless it is probably better to use this approach, and work with an estimate of B rather than to attempt to determine accurately the birth function for each age class of ewes on the basis GRUBB'S data.

With regard to the value of B WILLIAMSON and BOYD (1960) give the average fecundity for ewes as 1.2, since they estimated

that about one fifth of ewes have twins, and they did not observe any cases of triplets. This was therefore the figure adopted in the model. It is probably a little too high since it appears not to take neonatal mortality into account. Nevertheless, as stated earlier, the process was initiated in the low population density situation where such mortality is much less than at high densities.

Finally it should be made clear that the increase of neonatal mortality with population density is regarded as a reduction in the birth rate rather than as an increase in the death rate. It is thus taken into account by the component $1 - \frac{i}{N}$ of the birth function $\lambda(x,t)$. This viewpoint is in agreement with that of GRUBB, who although recording the total number of offspring, only includes those who survive the neonatal period in the construction of his life-tables. Likewise BOYD's data does not take into account those lambs who do not survive this period.

6.4.5 The Death Functions

The death functions take the form

$$\mu_1(x,t) = \theta_{21}(x)\phi_2(t)$$

for males, and

$$\mu_2(x,t) = \theta_{22}(x)\phi_2(t)$$

for females. The functions $\theta_{21}(x)$ and $\theta_{22}(x)$ can be derived in a standard way from their corresponding survivorship functions $\ell_1(x)$ and $\ell_2(x)$.

Thus for any mortality function $\theta(x)$ the associated survivorship function $\ell(x)$ is related to it by

$$\ell(x + \delta x) - \ell(x) = - \theta(x)\ell(x) + o(\delta x)$$

and hence by

$$\theta(x) = - \frac{d}{dx} \left\{ \ell n \left(\ell(x) \right) \right\} \qquad (1)$$

Here $\ell_1(\cdot)$ and $\ell_2(\cdot)$ are polynomials of an appropriate order fitted to GRUBB's generalised life-tables referred to earlier, which again must be assumed to be typical of the island as a whole.

Previous remarks about the annual mortality pattern of the Soay sheep on Hirta indicate that $\phi_2(t)$ should be prescribed as

$$\begin{aligned} \phi_2(t) &= m(t'') \quad \text{for} \quad 0 \leqslant t'' \leqslant 3, \\ &= 0 \text{ otherwise,} \end{aligned} \qquad (2)$$

where $t'' = t - 12 \left[\frac{t}{12} \right] - 1$, and where the function $m(t'')$ is normalised to

$$\int_0^3 m(t'')dt'' = 1$$

GRUBB also records the timing of mortality for 1965 and his data shows a wide dispersion over February to April. The function $m(t'')$ was therefore assumed to be uniform over the interval $[0,3]$ of t''. This is, of course, a little artificial, but the results of some preliminary simulations with a simple unimodal form for $m(\cdot)$ did suggest that its exact form is of only secondary importance, though again to put this remark on a strict quantative basis would require a lot of extra computer time.

6.4.6 The Carrying Capacity of Hirta

The meaning of the term 'carrying capacity' in the literature is often obscure. Implicitely it appears to be some kind of equilibrium level of the population, akin to the quantity $N(1 - \rho)$ of the basic SL model. In general, however, most ecosystems, and certainly the sheep population of Hirta, do not possess such fixed equilibria and this connept is therefore an unreal one.

It is thus more satisfactory to define the carrying capacity similarly to the quantity N of the model. In ecological terms it is therefore the maximum level that the population can possibly attain, if only briefly, under the most favourable natural conditions. In the context of the model, previous simulations of the SL process have shown that the probability of this level ever being attained is extremely small, even over a long period of time. Nevertheless it is the definition which we will continue to adopt here as it is quite free of all ambiguity.

An examination of BOYD's (1974) data taking into account its general upward trend, and the conclusions of other field workers about feral sheep population densities, suggest that future maxima on Hirta are likely to have a long term average of about 2000. Having then assigned the initial age distribution and birth and death functions to the model it is then a straightforward matter to determine by trial and error a suitable value of N. In fact the value $N = 2500$ was found to be satisfactory.

6.5 COMMENTS ON THE RESULTS OF THE FITTED SLTA MODEL

As is clear from Table 6.2 and also Fig. 6.1 the simulated results from the fitted SL model whose construction has been described do not at all reflect the cyclic pattern of BOYD's data. This might well be expected, not only intuitively, but also on account of some of the simulated results of the simpler versions of the SL model described in the previous chapters.

This does not mean, of course, that quite low population levels may not occur from time to time. Thus, for example in Table 6.3, there is a recorded minimum of 642 when a little over 30 years of the communities life is simulated by this model, and no doubt much lower minima might well occur if substantially longer periods of time were considered. Indeed, as has been emphasised before, extinction is always a possibility however slight, and it is in this fundamental way that the stochastic model differs from its deterministic counterpart.

Nevertheless on the basis of the results obtained it is clear that the probability of the model exhibiting a persistent cyclic pattern over a long period of time is so small, that it cannot be accepted as adequately describing the general population development in time.

In simple ecological terms one can argue that the reason for this is that it does not take into account the sharp increase in the death rate that will occur if the population level, j, is above a certain critical value N_C, say, at the onset of winter. The island can maintain a population total substantially greater than N_C up to the end of the year, but then many individuals will have insufficient stored energy to see them through the critical period at the

beginning of the next. In this way the population is left stranded.

Neither can this aspect of the population dynamics of the community be taken into account merely by appending a factor such as $(1 + \frac{j}{N})$ to the death functions. In that case the overall behaviour would be much as before. No cyclic pattern would emerge.

To achieve greater reality therefore the model must be modified in a more fundamental way, which will now be described.

6.6 A MODIFIED SLTA MODEL

The birth function is unaltered, but the death functions are now

$$D_\ell(x,t) = d\mu_\ell(x,t) \quad \text{when} \quad j \geq N_c \quad \underline{\text{and}} \quad 0 \leq t_C \leq 12,$$
$$= \mu_\ell(x,t) \text{ otherwise,}$$

where $\ell = 1,2$ for males and females respectively, d is a constant ≥ 1, and where $t_C = t - 12\left[\frac{T_c}{12}\right] - 12$, and T_C is the value of t at the last instant at which the state $j = N_c$ was entered.(*)

This model was run initially with trial values of d and it soon became apparent that relatively large values of d (> 5) would have to be adopted if oscillations comparable in amplitude to those of BOYD's data were to show up. In Table 6.2 there are results for $d = 5$, 10, 20, 50, and 100 and these may be compared with those for the unmodified model ($d = 1$), and the real data. Also a graphical comparison of the cases $d = 1$, 5, 10 and the real data is shown in Fig. 6.1, and of $d = 20$, 50, and 100 in Fig. 6.2.

(*) Here again, $[x]$ means the integral part of x.

The cases d = 5 and d = 10 are of special interest since they do show a periodicity in approximate agreement with that of the actual population profile. Clearly their levels are running too high, but this is probably due to N_c taken as 1800 in the model, being too large rather than N or b. This point would be worth further investigation.

For the larger values of $d(\geq 20)$ the catastrophic effect of j increasing beyond Nc becomes more pronounced. At d = 50 the population only just escapes extinction at the first crash, and in the case d = 100 it does become extinct after only five years.

Note that the period of the oscillation also increases on average with d, at least for $d \geq 5$. Thus its average value is a function of d and presumably of N_c as well. Since, however, the value of d must depend to some extent on climatic factors, it would be more realistic to represent it as a random variable.

In any case the time T_M between successive population maxima, in excess of 1200, say, both in the model and in reality is certainly a random variable and on the basis of BOYD's data its mean appears to be about 4 years with a standard deviation of about $\frac{1}{2}$ year. It is of course incorrect to regard it as a fixed quantity as might be implicit in a deterministic analysis.

6.7 EXTENDING THE USE OF THE MODIFIED SLTA MODEL

Clearly it will be of interest to extend the use of the model to simulating longer periods of the populations life. However, if computer time requirements were to be kept within reasonable limits,

then taking into account the number of cases to be considered it was not found possible to cover a period of more than about 30 years when $d = 1$, and about 20 years for $d \geq 5$ for Hirta.

Some further results are shown in Table 6.3 where also are recorded not only maximum and minimum levels for the population as a whole, but also separately for males and females. These results imply that the expected minimum level of the total population attained over a given period of time would not be much affected by changes in the value of d for $1 \leq d \leq 10$. Thereafter the expected minimum decreases as d increases.

Stated in probability terms this would imply that for a given period of time the probability of extinction is essentially independent of d for $d \leq 10$, but then increases with d. To determine the form of this dependence by adequate simulation, and no other method is possible, would require enormous amounts of computer time, and this was not attempted therefore.

By appropriate scaling of parameters where necessary the model can readily be used for the sheep population of Soay and Boreray. Actually as the population levels there are much lower on average than on Hirta, then in general the holding times between events are correspondingly greater, and so also therefore is the real time to computer time ratio. Thus for Soay periods of up to 170 years have been considered and for Boreray periods of up to 220 years.

The results obtained for these islands indicate that the remarks made above about the dependence of minimum population levels on d apply to these smaller populations as well. Nevertheless even for $d = 1$ both populations came near to extinction with each attaining a minimum of 17 males.

The results for Dun, the smallest of the St. Kilda islands, clearly imply a precarious existence for any sheep community there. If there has been such a community which subsequently became extinct, then this could be simply a reflection of the chance mechanisms of the SL process. No special external adverse events need have occurred.

It is now appropriate therefore to consider the final and obvious question as to how fortunate the original flock of sheep on Soay has been to survive the last millenium, or for that matter what are its chances of surviving the next. Such a question can now be answered, at least provisionally, by the model. This was not attempted however, since not only would very large amounts of computer time be required, even though there is some alleviation of this problem for the smaller islands, but also as pointed out in the discussion there are certain aspects of the ecosystem which have not yet been taken into account, and the extent of whose influence on the population development, supposedly slight, has not in fact been properly established. Nevertheless it does appear that the modified SL model could provide an adequate theoretical framework for further studies of the sheep population of St. Kilda, and perhaps of other isolated communities as well.

Table 6.1 J.M. BOYD'S data for the Soay sheep of Hirta.

	Ewes	Lambs	Rams	Total
1952				1114
1955				710
1956				775
1957				971
1958				1099
1959	722	458	164	1344
1960	448	86	76	610
1961	417	417	76	910
1962	624	221	211	1056
1963	821	526	243	1590
1964	654	237	115	1006
1965	753	567	149	1469
1966	918	495	185	1598
1967	593	231	52	876
1968	571	415	118	1104
1969	770	357	70	1197
1970	633	351	78	1062
1971	855	753	175	1783
1972	747	600	207	1554
1973	809	482	109	1400

Table 6.2

Comparison of simulated with actual population total for various values of d.

		Values of d					
	Actual	1	5	10	20	50	100
1955	710	702	702	702	702	702	702
1956	775	1121	1115	1153	1130	1110	1138
1957	971	1276	1284	1341	1285	1298	1340
1958	1099	1526	1540	1613	1557	1561	1609
1959	1344	1742	1768	1794	1789	1762	1832
1960	610	1895	1951	1962	1971	1947	8
1961	910	2040	1550	1093	729	77	
1962	1056	2126	1810	1525	1137	171	
1963	1590	2153	1773	1806	1501	272	
1964	1006	2186	2024	1178	1798	388	
1965	1469	2124	1384	1530	1967	536	
1966	1598	2029	1663	1750	257	715	
1967	876	1964	1834	1967	493	901	
1968	1104	1933	1423	852	617	1146	
1969	1197	1904	1698	1231	820	1315	
1970	1062	1855	1886	1499	1056	1558	
1971	1783	1814	1439	1776	1357	1826	
1972	1554	1794	1816	2043	1646	365	
1973	1400	1850	1583		1923	738	

The value d = 1 defines the unmodified model.

TABLE 6.3

Shows simulated maxima, minima, time to extinction etc., for each island for various values of d.

Values of d.

1	5	10	20	50	100	
1,0	1,0	1,0	1,0	1,0	1,1	HIRTA
363	231	208	265	220	$\hat{\tau} = 60, \hat{\sigma} = 0$	
2248, 1020, 1450	2031, 754, 1339	2047, 788, 1330	1982, 785, 1330	1954, 757, 200	1834, 693, 1140	
642, 136, 506	633, 132, 50	642, 133, 508	235, 32, 198	76, 3, 71	0, 0, 0	
1,0	1,0	1,0	1,0	8,8	5,5	SOAY
2080	1320	1320	1250	$\hat{\tau} = 149, \hat{\sigma} = 52$	$\hat{\tau} = 188, \hat{\sigma} = 25$	
392, 160, 257	324, 132, 236	325, 157, 215	332, 139, 235	134, 36, 97	148, 41, 106	
96, 17, 61	104, 22, 78	86, 12, 59	28, 2, 24	(61, 28, 32)	(74, 32, 43)	
1,0	1,0	1,0	1,0	5,5	5,5	BORERAY
2610	1670	1670	1610	$\hat{\tau} = 142, \hat{\sigma} = 44$	$\hat{\tau} = 251, \hat{\sigma} = 149$	
291, 134, 197	249, 112, 197	252, 116, 214	246, 109, 172	113, 33, 78	174, 69, 115	
63, 17, 31	75, 14, 53	60, 10, 50	30, 1, 20	(58, 30, 28)	(74, 41, 42)	
1,0	1,0	1,1	5,4			DUN
5040	3450	$\hat{\tau} = 2370, \hat{\sigma} = 0$	$\hat{\tau} = 519, \hat{\sigma} = 635$			
125, 14, 92	108, 54, 86	108, 55, 80	62, 25, 46			
28, 4, 14	31, 5, 18	(0, 0, 0)	(34, 22, 25)			

See over for notes on Table 6.3

NOTES ON TABLE 6.3

In each rectangle two numbers in first line denote number of runs of the case, and number of cases of extinction, respectively. If no cases of extinction occur, the number in the second row denotes simulated time in months. If extinction does occur then numbers in second row are mean and standard deviation of realized extinction times. Numbers in third row, in each rectangle, give maximum (or average of maxima if there is more than one run of the case) of population total, number of males and number of females respectively. Numbers in the last row are the corresponding minima, if no cases of extinction occur. Otherwise, they are the corresponding standard deviations of the realised maxima.

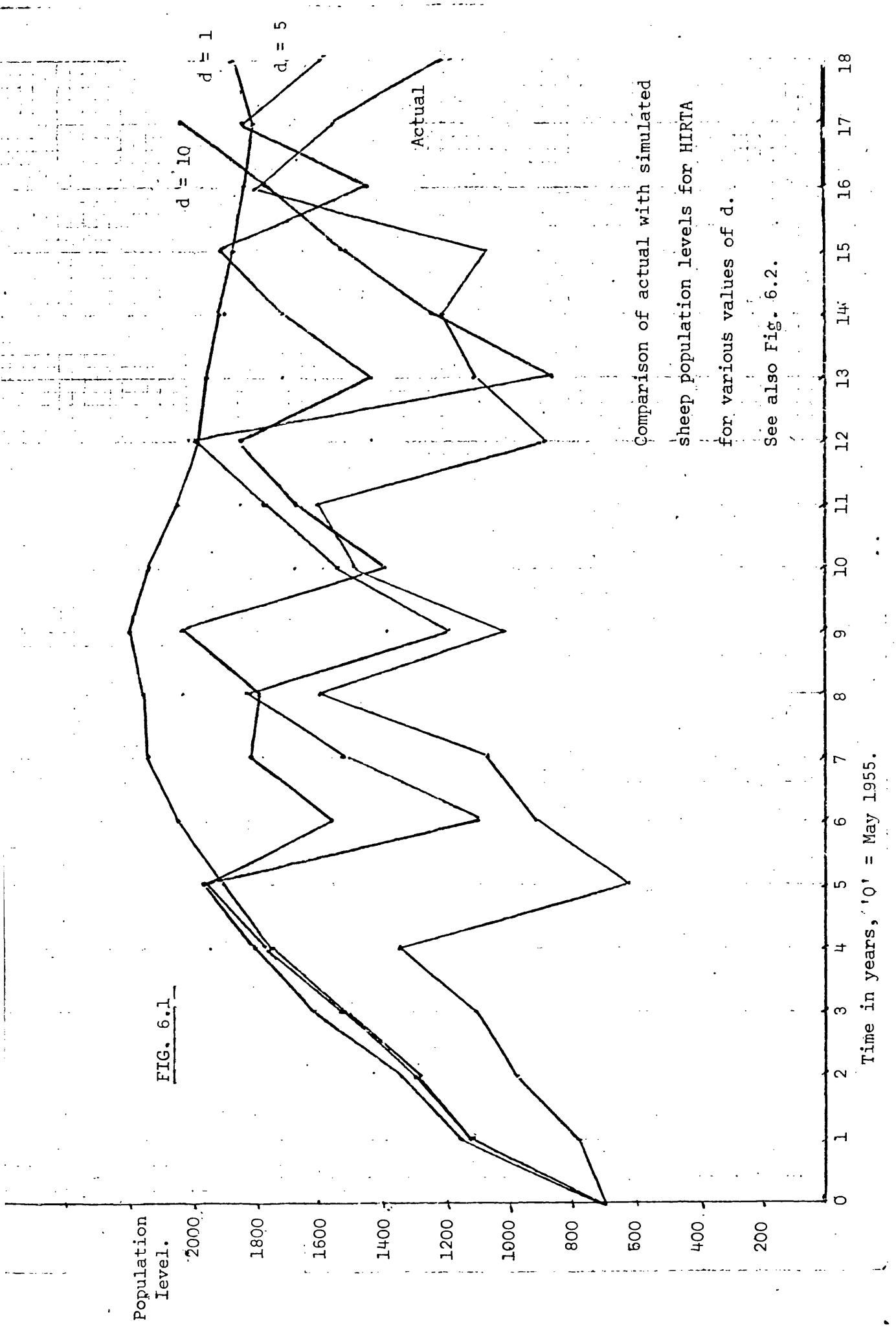


FIG. 6.1

Comparison of actual with simulated sheep population levels for HIRTA for various values of d.

See also Fig. 6.2.

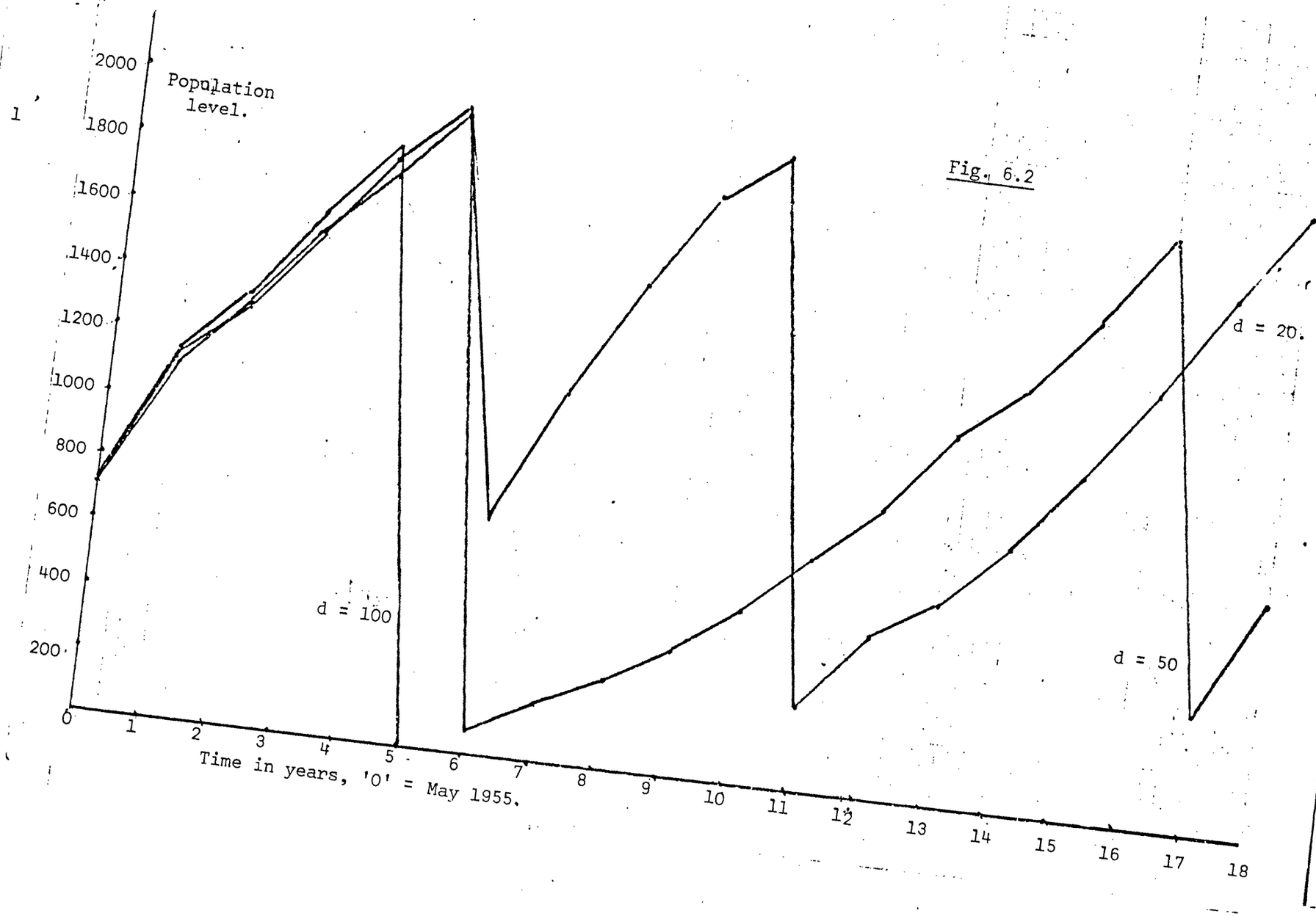

Population level.
2000
1800
1600
1400
1200
1000
800
600
400
200
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
Time in years, '0' = May 1955.
d = 100
d = 50
d = 20.

Fig. 6.2

APPENDIX 1

SIMULATION OF THE PROCESS SL(λ,μ,i,N)

When the population level is j the waiting time W_j to the next event has negative exponential density

$$\theta_j e^{-\theta_j x}$$

where $\theta_j = \lambda j(1 - \frac{j}{N}) + \mu j$

Thus in accordance with the standard theory, the random variable

$$\Xi = 1 - e^{-\theta_j W_j} \qquad (1)$$

is uniformly distributed on $[0,1]$, and so realisations of W_j are generated by

$$-\theta_j^{-1} \ln(1 - \Xi) \qquad (2)$$

This is essentially the method of NAG(*) routine G05ACF which was used throughout the simulation of this process.

Note that $E(W_j) = \theta_j^{-1}$ regarded as a function of j will decrease as j increases from 1, and for $\lambda > \mu$ attains a minimum value Θ^{-1} at $j = j_L$, such that $j_L = \eta$ if $\xi \leqslant \eta + 0.5$ and $j_L = \eta + 1$ if $\xi > \eta + 0.5$ where

$$\Theta = \frac{N}{4\lambda}(\lambda + \mu)^2 - \frac{\lambda\varepsilon^2}{N},$$

$$\varepsilon = \text{Min}(\xi - \eta, \eta - \xi + 1),$$

$$\xi = \frac{N}{2\lambda}(\lambda + \mu),$$

$$\eta = [\xi]$$

and where Min(x,y) is defined in the usual way as equal to x if $x < y$, and equal to y, otherwise.

---

* This overall designation applies to any routine from the Numerical Algorithm Group Mark 4 library of the South West Universities Computer Network.

Thus for $j_L \leq j \leq N$, $E(W_j)$ is an increasing function of j. On the other hand, if $\lambda \leq \mu$, $E(W_j)$ decreases with j for all j such that $1 \leq j \leq N$. Values of j_L for SL(λ,.1,10,100) for λ = .12,.13,.14,.15 and .2 are shown in Table A1.1. Nevertheless the results of Table A1.2 for the means and standard deviations of the corresponding maxima indicate that for $\lambda \leq 1.5\mu$ the probability p_L^*, say, of the process level j attaining j_L is small. More precisely, it appears that p_L^* is an increasing function of λ for $\lambda \geq \mu$, but is les than .01 so long as $\lambda \leq 1.5\mu$. On the other hand, for $\lambda = 2\mu$ it is very near to 1.

The construction of the appropriate probability distribution of events at the end of the waiting period W_j is straightforward. If u is a realised value of the random variable U, uniformly distributed on [0,1], then the next event will be a birth if

$$0 \leq u \leq \frac{b_j}{b_j + d_j}$$

and a death otherwise, where $b_j = \lambda\left(1 - \frac{j}{N}\right)$ and $d_j = \mu j$. The generation of random numbers u was effected throughout by NAG routine G05AAF.

The program, as is the case with all others used in this research, is written in the FORTRAN language. It contains no special difficulties and is not exhibited here therefore. A scheme of the simulation, however, is shown in Fig's. A1.1, A1.2 and A1.3. The notation there, it is hoped, is largely self-explanatory. Thus with reference to Fig. A1.1 the run variables are J, the realised process level at time T; W, the waiting time between events; MAX and MIN, the current greatest and least values of J within the run, and K, the number of steps taken since the start of the run. Thus the initialisation of run variables takes the form J = I, MAX = I, MIN = I, T = 0, W = 0 and K = 0.

The subloop OBS records the process level X(L) at the preassigned instant R(L), L = 1,2,...,LMAX, for which $T \leq R(L) < T + W$. See Fig. A1.3. In order to choose appropriate values for R(L), which need not be equally spaced, and for LMAX, it is necessary to have some idea of the mean time to extinction. This may be obtained from the theory, or alternatively, by pilot runs. In any case, in view of the time-sequential nature of the process, it is not necessary to run through all the LMAX values of R(L) after each jump. It is only necessary to continue from the previous value of L up to the first L for which $R(L) > T + W$. Thus the inclusion of the subloop OBS, which is most important if an emprical understanding of the distribution of states at a general instant is to be obtained, does not require much extra computer time, - about 2% at most.

A run continues until K = KMAX, unless previously J = 0, in which case the jump loop is vacated immediately. Each time the jump loop is completed, one way or another, the case variables are adjusted accordingly. Note, however, that SMIN and SSMIN only accumulate over those runs for which extinction does not occur. On the the other hand, STE and SSTE are the sums and sums of sqares of extinction times in contrast to ST and SST which sum over all runs regardless of whether extinction occurs or not. Similarly SKE and SSKE are the sums and sums of sqares of the number of jumps to extinction, whereas SK is the sum of all jumps over all runs regardless of whether extinction occurs or not.

As the simulation proceeds runs are indexed by the integer variable IR and the run loop is vacated when TR = NR, the prescribed number of runs. It then remains to compute the case results which are as follows.

1) The mean and standard deviation of the run times(*) from STE and SSTE, and the mean and standard deviation of the number of jumps, from SKE and SSKE, for those runs where extinction does occur.

2) The mean and standard deviation of all waiting times, W, over all runs, from SK,ST and SST.

3) The mean and standard deviation of the realised minima over those runs where extinction does not occur, from SMIN and SSMIN.

4) The mean and standard deviation of the realised maxima over all runs, from SMAX and SSMAX.

5) The mean, standard deviation, skewness and kurtosis of the, at most, NR realised values of X(L), for L = 1,2,...,LMAX. These are calculated from the sums M(S,L), S = 1,2,3,4 and L = 1,2,...,LMAX.

Actually, the quatities (2) are included only to provide an order of magnitude check on the correct generation of waiting times. Otherwise they are of little interest.

All the simulations of the basic SL process, apart from a few developement runs, were carried out on the CDC 7600 computer at ULCC. It was found that about 40,000 jumps could be excuted in 1 second of CP time of that machine.

(*) By this is meant simulated real time, and not, of course, computer CP time.

TABLE A1.1

Values of j_L for various λ where $\mu = 0.1$ and $N = 100$.

λ	.12	.13	.14	.15	.16	.17	.18	.19	.20
j_L	92	88	86	83	81	79	78	76	75

TABLE A1.2

Mean and standard deviation of maximum level attained over R runs(*) of the SL process for various λ, i and N, where $\mu = 0.1$.

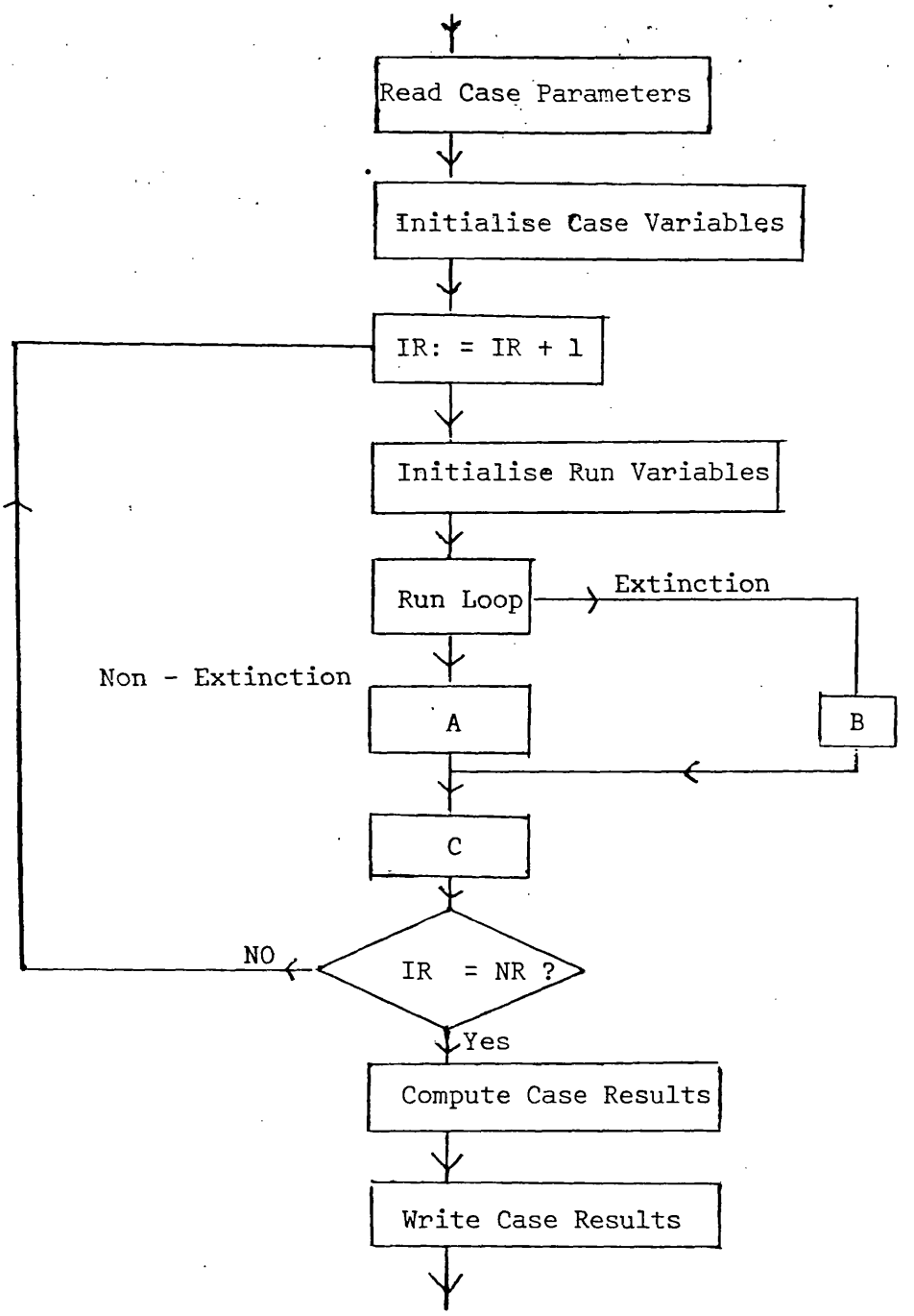
In each rectangle, upper number = mean, second number = standard deviation and number in brackets = value of R.

	λ = .11	.12	.13	.14	.15
i = 10, N = 100	19.4 7.56 (50)	25.6 9.69 (50)	34.6 13.8 (50)	46.2 15.5 (50)	59.3 11.6 (50)
i = 10, N = 200		40.6 20.0 (50)			
i = 100, N = 1000		274.3 10.3 (10)			
i = 1000, N = 10000		1199 24.1 (10)			

(*) Each run was taken to the zero state.

FIG. A1.1

BASIC SCHEME OF SIMULATION OF SL AND SIMILAR PROCESSES



NR = prescribed maximum number of runs for a case.

IR indexes runs throughout simulation of a case.

At A: SMIN = SMIN + MIN, SSMIN = SSMIN + MIN*MIN

At B: STE = STE + T, SSTE = SSTE + T*T; SKE = SKE+K, SSKE=SSKE+K*K

At C: SK = SK + K, ST = ST + T; SST = SST + SSW,

SMAX = SMAX + MAX, SSMAX = SSMAX + MAX*MAX, M(S,L) = M(S,L) + X(L)**S

FIG. A1.2

SCHEME OF RUN LOOP

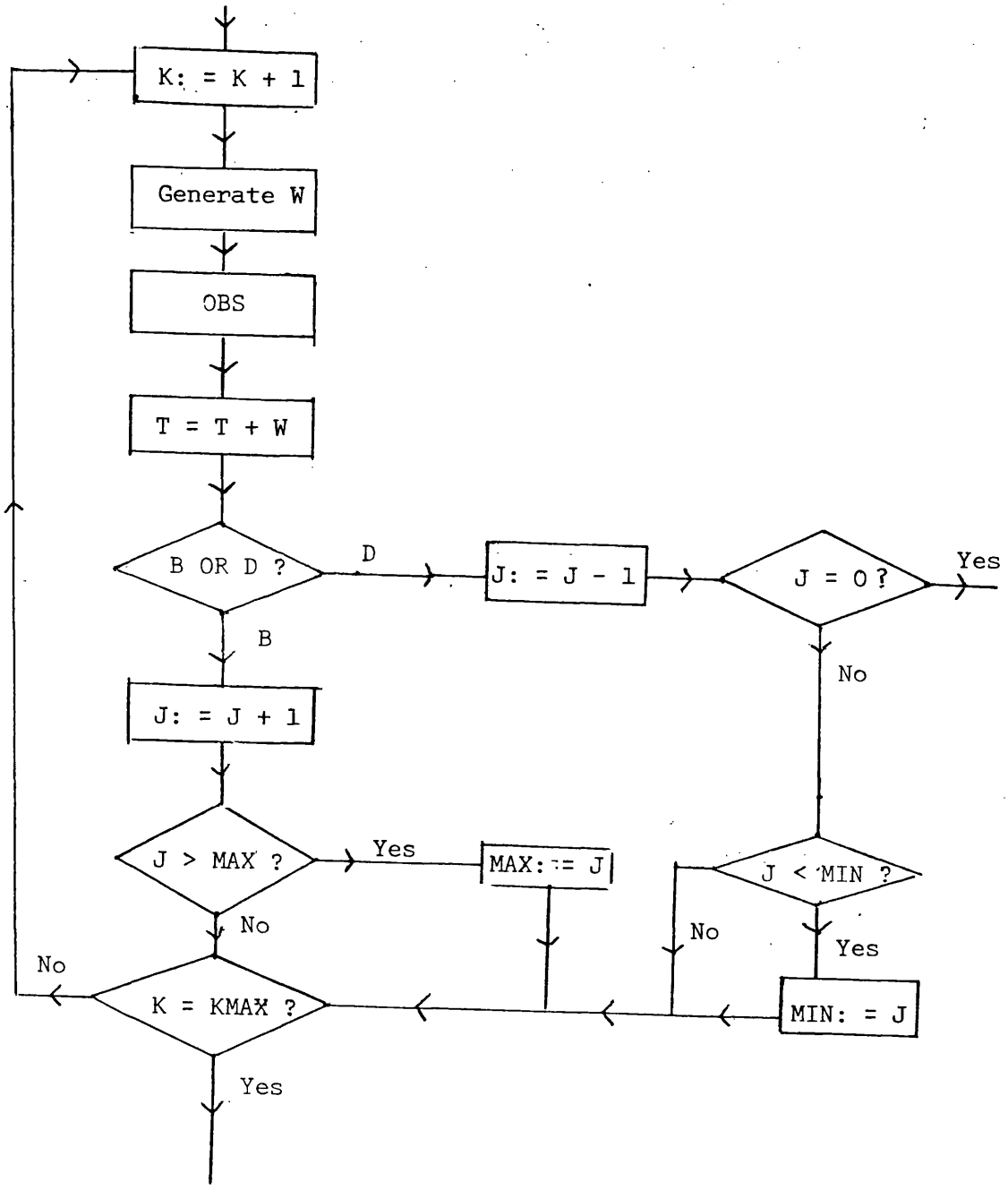
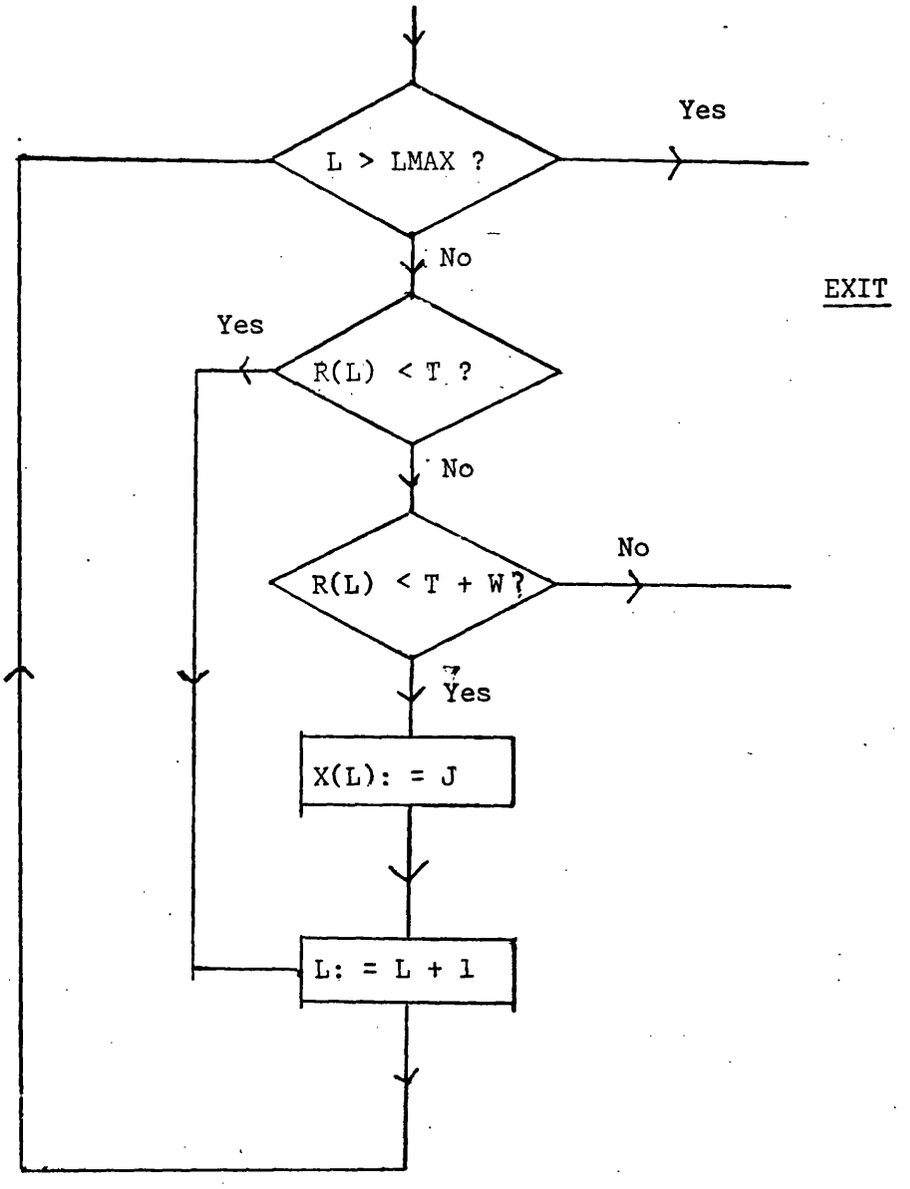


FIG. A1.3

SCHEME OF 'OBS' LOOP



APPENDIX 2

SIMULATION OF THE SLT MODEL

In the case of the SLT process the birth function $b\{1 + a\sin(\omega t)\}$ must be evaluated at the time of occurence of each event, i.e. at the start of each waiting period, W_j. Also the generation of values of W_j is a good deal more complicated than in the case of the basic SL model where the birth and death parameters are independent of t. There is no explicit form for W_j corresponding to equation A1(2).

Instead values, w, of W_j (= W) are obtained iteratively as solutions of equation 5.4(3). The scheme of iteration which is essentially a standard NEWTON-RAPHSON procedure, is shown in Fig. A2.1 Here,

$$F \equiv \theta_j w + \frac{abj}{\omega}(1 - \frac{j}{N})\left[\cos(\omega t) - \cos\{\omega(t + w)\}\right] + \ln(1 - v) \qquad (1)$$

where v is a realised value of the random variable V uniformly distributed on $[0,1]$, and $\theta_j = bj(1 - \frac{j}{N}) + \mu j$. Also,

$$DF \equiv \theta_j + abj(1 - \frac{j}{N})\sin\{\omega(t + w)\} \qquad (2)$$

The initial value assigned to W at the start of the iteration procedure is

$$w_o = -\theta_j^{-1}\ell n(1 - v) \qquad (3)$$

i.e. the waiting time that would occur if the birth function contained no harmonic component.

That the equation F = 0 has a unique positive root w when $1 \leq j < N$ and $0 \leq a < 1$ is easily seen by observing that when w = 0 $F = \ln(1 - v) < 0$, and also that DF > 0 for all w. If a = 1, then again subject to $1 \leq j < N$, DF can only be zero when $w = \frac{k\pi}{\omega} - t$

(k any integer), but otherwise is strictly positive, so again there is a unique positive root.

In the very exceptional case where $j = N$, we have simply that $F = \mu Nw + \ln(1 - v)$, so that clearly the equation has a unique solution $w = -\ln(1 - v)/Nw$. No iteration is then necessary.

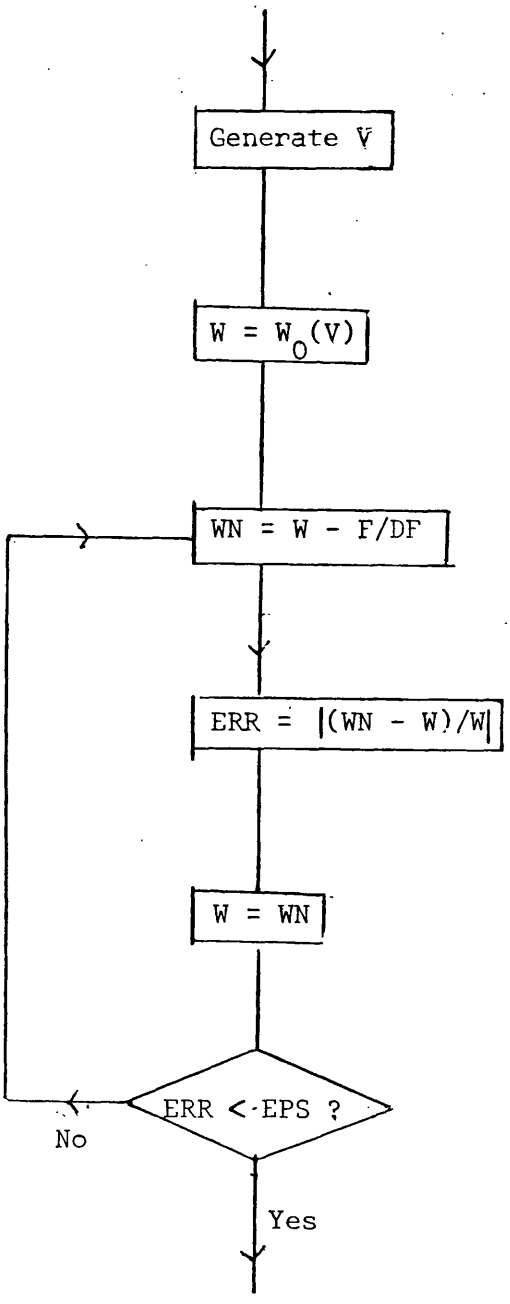
Thus for all j such that $1 \leqslant j \leqslant N$ and all a such that $0 \leqslant a \leqslant 1$ and all $b > 0$ there is a unique positive solution of the equation $F = 0$.

The rate of convergence of the algorithm depends, of course, on the value of EPS. It was found, for example, that for EPS = 10^{-3} only 2 iterations were required for most cases. However, substantially more iterations may be necessary if v is near to 0, since then $\ln(1 - v)$ is also near to 0. For EPS = 10^{-6}, the adopted value, about 4 to 6 iterations where found to be necessary, in general.

The need to carry out such an iteration scheme for each waiting period increases the computer time required by an order of magnitude as compared with the basic SL model. In fact it was found that only about 1600 jumps could be effected in 1 second of CP time on the SWURCC 2980 machine. Since therefore this computer is about 4 times slower than the CDC 7600 at ULCC, then it follows that in absolute terms the simulation of the SLT model takes about 6 times longer than an equal number of jumps in the SL model.

FIG. A2.1

GENERATION OF WAITING TIMES W FOR THE SLT PROCESS



The random variable V is uniformly distributed on [0,1]. Also, F,DF and $W_0(V)$ are defined by equations A2(1),(2) and (3) respectively.

APPENDIX 3

SIMULATION OF THE SLA AND SLTA PROCESSES

A3.1 THE SLA PROCESS

The overall scheme of simulation described in Fig. A1.1 remains essentially the same as before, but the inner structure of the run loop as shown in Fig. A1.2 must necessarily be altered substantially in order to take account of the seprarate age-class totals. The modified version is shown in Fig. A3.1.

As in the SLA process the birth and death rates are independent of t, then with reference to equation 5.6(1) in the main text, the function $g_j(x,t)$ takes the form $\theta_j(x)$, in which case

$$h_j \equiv h_j\{u|z(x,t),t\} = \int_0^\infty \theta_j(x+u)z(x,t)dx \qquad (1)$$

Thus as long as $0 \leq u < \delta$ where δ is small and to be regarded as tending to zero,

$$h_j = \int_0^\infty \theta_j(x)z(x,t)dx + O(\delta)$$

subject only to the condition that there exists a constant $K > 0$ such that $|\theta_j'(x)| < K$ for all x such that $0 \leq x < \infty$.. This condition is certainly satisfied for the actual birth and death functions considered here, and indeed for any birth and death functions which are likely to be of interest. Hence in this situation we have simply,

$$h_j = e_j(t) + O(\delta) \qquad (2)$$

where $e_j(t)$ is the 'event rate' at the time t at which the waiting

period begins. That is if $(1 - \frac{j}{N})\lambda(x)$ and $\mu(x)$ are the t - independent birth and death rates, then

$$e_j(t) = b_j(t) + d_j(t) \tag{3}$$

where $$b_j(t) = (1 - \frac{j}{N})\int_0^\infty \lambda(x)z(x,t)dx$$

and $$d_j(t) = \int_0^\infty \mu(x)z(x,t)dx$$

Hence the distribution function of W conditioned on $W < \delta$ is

$$L_j^* = 1 - \exp\left[- e_j(t)w \right] + O(\delta) \tag{4}$$

i.e. within $O(\delta)$ is that of a random variable having the negative exponential density with parameter $e_j(t)$.

In the numerical context therefore the procedure to be adopted is as follows. Suppose there are C age-classes each of width a, and that n_ℓ ($\ell = 1,2,\ldots,C$) is the total number of individuals in the ℓ^{th} class immediately after the occurrence of an event. Also let

$$R = \sum_{\ell=1}^{C} \left[(1 - \frac{j}{N})\lambda_\ell + \mu_\ell \right] n_\ell \tag{5}$$

where λ_ℓ and μ_ℓ are, respectively the values of $\lambda(x)$ and $\mu(x)$ at $x = (\ell - 1)a + \frac{a}{2}$. Also let CT be a suitable fixed small positive quantity. Then if $EW = R^{-1} \leq CT$, W is assigned a realised value, w, of the negative exponential distribution with parameter R. Such values may be generated by NAG routine G05ACF as in the case of the SL and SLT processes.

Suitable values of a,C and CT must, to some extent, be determined empirically and they must also take into account the requirement that the probability that W exceeds a is small. In fact, it was found

satisfactory to take a = 2, C = 20 and CT = a/3ℓn10. This last condition ensures that $P(W > a) < 10^{-3}$.

The probability for the next event, birth (B) or death (D), is as described in Appendix 1 for the SL process, but now

$$b_j = (1 - \frac{j}{N}) \sum_{\ell=1}^{C} \lambda_\ell n_\ell \tag{6}$$

and

$$d_j = \sum_{\ell=1}^{C} \mu_\ell n_\ell \tag{7}$$

On the other hand, if EW > CT which is likely to happen in the cases considered here when $j \lesssim 10$, then instead the process is taken to time $T + \eta$ where $\eta = EW/Q$ and Q is sufficiently large. A suitable value for Q was found to be 20. The probability that a birth will occur at the end of the period η is $b_j\eta$, that a death will occur is $d_j\eta$ and that no event will occur is $1 - b_j\eta - d_j\eta$.

At the end of the end of period time W (or η) all age - class totals, n_ℓ, must be adjusted to take account of those individuals who have now moved into their next age - class. With reference to Fig. A3.1 this is effected at ADJ where the scheme of such transfers is as follows. (Note that W stands for W or η and that ζ, initialised to zero, is a residual time accumalator.)

$$\zeta \longrightarrow \zeta + W$$

and for $\ell = 1,2,\ldots,C$,

$$\delta n_\ell = \left[\frac{W n_\ell}{a}\right] \tag{8}$$

$$n_\ell \longrightarrow n_\ell + \delta n_{\ell-1} - \delta n_\ell \qquad (\delta n_o = 0) \tag{9}$$

$$\zeta \longrightarrow \zeta - \frac{a\delta n_\ell}{n_\ell} \tag{10}$$

where in (8), $[x]$ means integral part of x, in the usual way.

Further, if at the end of the time W a birth has occurred then, of course, n_1 must be adjusted to $n_1 + 1$. If a death has occurred, then it is assigned to the ℓ^{th} class with probability

$$p_\ell^{(d)} = \frac{\mu_\ell n_\ell}{d_j} \qquad (11)$$

Thus if u is the realised value, generated by NAG routine G05AAF, of the random variable U uniformly distributed on $[0,1]$, then, at G in Fig. A3.1. the ℓ^{th} class is chosen if

$$P_{\ell-1} \leq u < p_\ell^{(d)} \quad (p_o^{(d)} = 0) \qquad (12)$$

and n_ℓ is then decreased to $n_\ell - 1$. If no event occurs at the end of the period η then no further adjustment of the age - class totals is necessary.

Finally, J, MAX and MIN (Fig. A3.1) are adjusted as necessary in the same way as in the basic SL model, and again the run loop is vacated at once if J = 0.

In conclusion to the above description of the methodology for simulating the SLA process, it should be pointed out that it is not restricted to any particilar birth and death functions. Thus although, as described in the main text, the actual functions employed where $b\beta^2 x e^{-\beta x}$ and μ respectively, many other such functions could equally be used. The scheme of simulation is by no means restricted to this special case.

With regard to the amount of computer time required in order to simulate a prescribed number of runs of a given case, it is clear that in view of the nature of the routine G, this must depend on the age distributions that actually occur during the life of the process. It

cannot, therefore , be specified as an absolute number defined by the parameters of the case under consideration. In any case it will depend critically on C, the number of age - classes. In addition, there is also the factor that pushing the process forward in time by small prescribed amounts η, as is required when EW > CT, requires more computer time per jump by an order of magnitude, than to generate waiting times W directly. Thus for a run where $j \geq 10$, say, for most of the time, far more jumps can be simulated per unit CP time than for runs where the process level does not behave in this way.

Nevertheless, it was found that for most of the runs here only about 100 jumps could be simulated in 1 second of CP time on the SWURCC 2980 machine, or equivalently about 400 jumps on the CDC 7600 machine at ULCC. This is, of course, very slow when compared with the simulation of the SL, and even the SLT, processes described previously.

A3.2 THE SLTA PROCESS

In the case of the SLTA process, if $\lambda(x,t)$ takes the form $\theta_1(x)\phi_1(t)$ and $\mu(x,t)$ the form $\theta_2(x)\phi_2(t)$ then

$$h_j = (1 - \frac{j}{N})\phi_1(t + u)\int_0^\infty \theta_1(x + u)z(x,t)dx + \phi_2(t + u)\int_0^\infty \theta_2(x + u)z(x,t)dx \qquad (1)$$

Thus following the argument described above for the SLA process it follows that

$$L^* = 1 - \exp\left[- (1 - \frac{j}{N})\Phi_1(t,w)B_1(t) - \Phi_2(t,w)B_2(t) \right] + O(\delta)$$

where for i = 1, 2,

$$\Phi_i(t,w) = \int_0^w \phi_i(t + u)du$$

and $$B_i(t) = \int_0^\infty \theta_i(x)z(x,t)dx.$$

Hence waiting times, w, conditional on $W < \delta$ may be generated as solutions of

$$(1 - \tfrac{j}{N})\Phi_1(t,w)B_1(t) + \Phi_2(t,w)B_2(t) + \ell n(1 - u) = 0 \qquad (2)$$

where u is a realisation of the random variable U uniformly distributed on $[0,1]$.

The numerical procedure to be adopted is similar to that of the SLA process, as described in the previous section, and is as follows.

Let $$R = (1 - \tfrac{j}{N})\phi_1(t)\sum_{\ell=1}^{C} \theta_{1,\ell}n_\ell + \phi_2(t)\sum_{\ell=1}^{C} \theta_{2,\ell}n_\ell \qquad (3)$$

where $\theta_{1,\ell}$ and $\theta_{2,\ell}$ are respectively the values of $\theta_1(x)$ and $\theta_2(x)$ at $x = (\ell - 1)a + \frac{a}{2}$, and n_ℓ is the ℓ^{th} age - class total immediately after the last event, or completion of a time interval η. Then if $R^{-1} < CT$ determine the waiting time to the next event as a solution of equation (2), above. The probability scheme for the event at the end of this waiting period is as for the SLA process except that now b_j and d_j are defined as

$$b_j = (1 - \tfrac{j}{N})\phi_1(t)\sum_{\ell=1}^{C}\theta_{1,\ell}n_\ell \qquad (4)$$

and $$d_j = \phi_2(t)\sum_{\ell=1}^{C}\theta_{2,\ell}n_\ell \qquad (5)$$

If $R^{-1} > CT$, which is likely to happen if $j \leq 10$ then again proceed as in the SLA process for this situation .

Now as in the actual simulations carried out $\theta_1(x) = b\beta^2 x e^{-\beta x}$, $\phi_1(t) = 1 + \alpha\sin(\omega t)$, $(0 < \alpha \leq 1)$ and, as previously, $\mu(x,t) \equiv \mu$, a constant, then equation (2) becomes,

$$(1 - \frac{j}{N}) \left\{ w + \alpha\omega^{-1}\left[\cos(\omega t) - \cos\{\omega(t + w)\}\right] \right\} \sum_{\ell=1}^{C} \theta_{1,\ell} n_\ell$$

$$+ \mu j w + \ell n(1 - u) = 0. \qquad (6)$$

This is essentially of the same form as equation 5.4(3) and may be solved by the NEWTON - RAPHSON method as described in Appendix 2.

The computer CP time required to simulate the SLTA process is, as would be expected, substantially more, in general, than that required for the SLA process, but its exact specification in terms of given parameter values is not possible. The reason is, as in the case of the SLA process, that it depends as well on the actual values of j, the process level, and also the age distributions that occur during the life history of the process. However, it does appear that if ξ, say, is the ratio of the CP time required to simulate a given number of jumps for the SLTA process to that required to simulate the same number of jumps for the SLA process, then so long as $j > 10$ the value of ξ is about 10. This is in line with CP requirements for the SLT process as compared with that for the SL process.

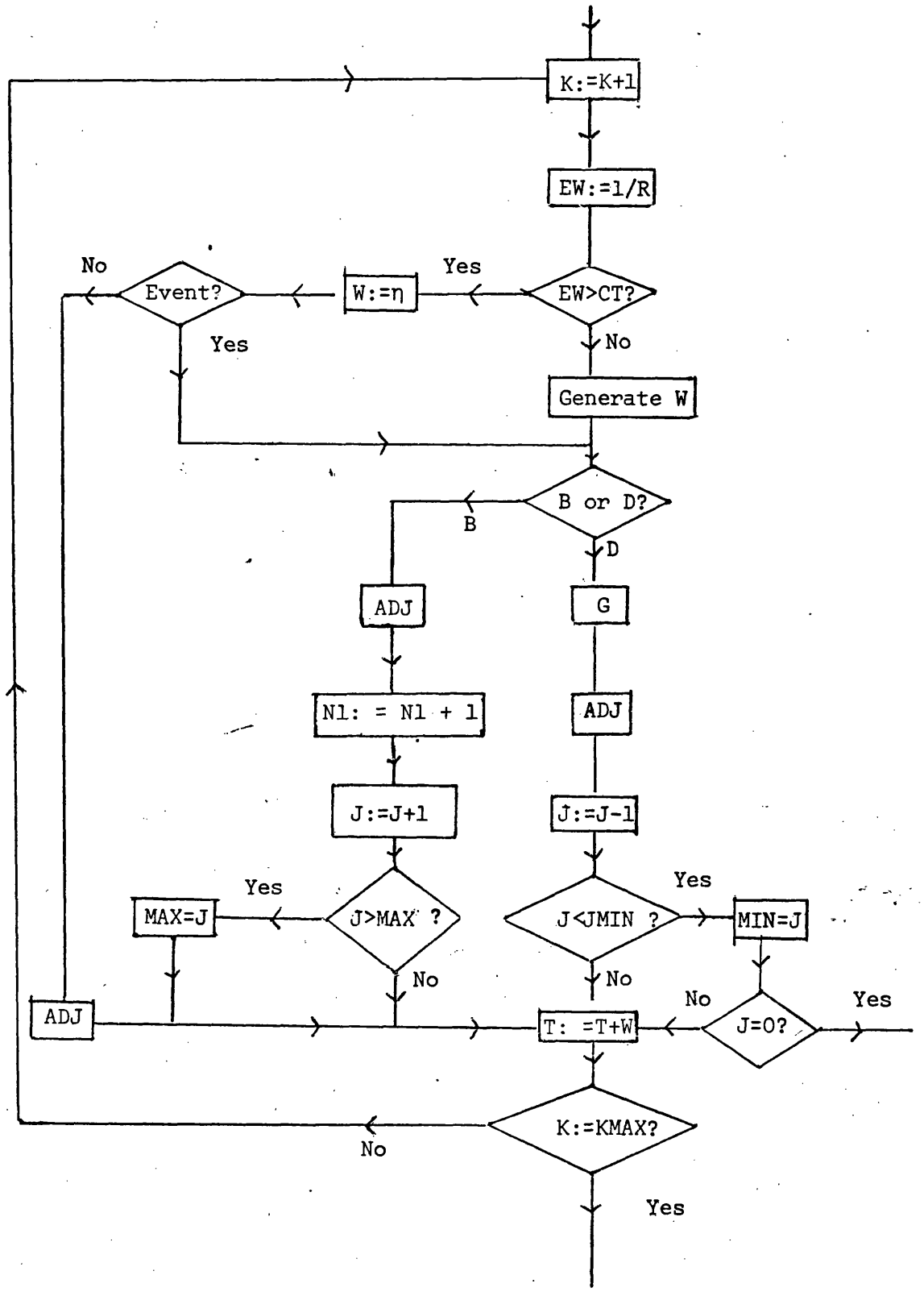
On the other hand, if j is generally less than 10 throughout the life spans of the SLTA and SLT processes, then it would be found that ξ is only a little greater than 1. The reason for this large difference in the value of ξ between these two situations is that in the latter case, in accordance with the scheme, the processes are taken forward in time by the small amount η, and the amount of additional evaluation that the computer must carry out in respect of

relatively small.

the time - dependent components $\phi_1(t)$ and $\phi_2(t)$ in the birth and death functions, respectively, is then relatively small.

FIG. A3.1

SCHEME OF RUN LOOP FOR SLA AND SLTA PROCESSES.



APPENDIX 4

SIMULATION OF THE SHEEP POPULATIONS OF ST. KILDA.

Although as stated in the main text it is necessary to deal with the male and female age - class compositions and totals separately, nevertheless again, the overall scheme of simulation exhibited in Fig. A1.1 remains essentially the same. The main modifications occur at A and C where sums such as SMIN,SMAX etc., and also M(S,L) must be evaluated for each sex. Also for most cases it is not possible, in view of computer requirements, to take NR, the number of runs for a given case, greater than 1. This is certainly true for the A1 age specification described in Section 6.4.2.

However, substantial changes and some simplification are necessary in the jump loop. (See Fig. A4.1.) In the first place, an equation such as A3.2(6) for the generation of waiting times, W, between events, would be excessively complicated in this context, and its solution could involve numerical stability problems. Instead, the process is pushed forward in time by successive small amounts η, as in the case of the SLA and SLTA processes when $j \leqslant 10$, whatever the current situation.

The probability scheme for the possible outcomes birth, death or non - event at the end of each time increment η is as in the case of the SLA and SLTA processes, but now with $\phi_1(t),\phi_2(t),\theta_1(t),\theta_{21}(x)$ and $\theta_{22}(x)$ defined as in sub - sections 6.4.4 and 6.4.5,(*)

(*) The subsequent argument will assume a common age - class interval width of a. It can, however be modified in an obvious way if, as in the case of the A2 age specification, the age classes are of unequal width.

$$b_j = (1 - \frac{j}{N})\phi_1(t)\sum_{\ell=1}^{C}\theta_{1\ell}n_{2\ell}$$

and $$d_j = \phi_2(t)\sum_{\ell=1}^{C}\left[\theta_{21\ell}n_{1\ell} + \theta_{22\ell}n_{2\ell}\right]$$

where $\theta_{1\ell}, \theta_{21\ell}$ and $\theta_{22\ell}$ are the values of $\theta_1(x), \theta_{21}(x)$ and $\theta_{22}(x)$ evaluated at $x = (\ell - 1)a + \frac{a}{2}$, and where $n_{1\ell}$ and $n_{2\ell}$ are the number of males and females respectively in the ℓ^{th} class at the beginning of the incremental time period of duration η.

In the event of a death occurring the procedure G operates as described in A.3.1, equations (11) and (12), but now

$$p_\ell^{(d)} = \frac{d_\ell}{d_j}$$

where $$d_\ell = \phi_2(t)\left[\theta_{21\ell}n_{1\ell} + \theta_{22\ell}n_{2\ell}\right]$$

On the other hand, the routine ADJ must be changed from the form adopted in the age - dependent processes previously considered. In their case, for most of the life history of the process there are few empty age classes and so the assumption implicit in the ADJ procedure described in Appendix 3, that the distribution of age within each age - class is uniform is satisfactory. Even then however, there may be a little distortion of the overall age distribution when the total population level, j, is low. In the model of the sheep populations of ST. KILDA however, in view of the nature of the natality data, at any given instant of time most age classes are empty, and the assumption of a uniform age distribution within each age - class is thus untenable. In fact, preliminary runs did show that its application led to a spurious dispersion of the age distribution, as would be expected.

A satisfactory alternative is to work with two totals within each age group. Suppose therefore that in the ℓ^{th} male age - class

($\ell = 1,2,\ldots,C$), the total number of 'more recent arrivals' to the class is $n_{11\ell}$ and that $n_{12\ell}$ is the total number of 'less recent arrivals'. Thus $n_{1\ell} = n_{11\ell} + n_{12\ell}$, and if further the initial male age distribution is $\left\{n_{1\ell}^{(0)}\right\}_{\ell=1}^{C}$ then at the start of the run set $n_{11\ell} = 0$ and $n_{12\ell} = n_{1\ell}^{(0)}$ for $\ell = 1,2,\ldots,C$. A similar procedure is adopted in each of the female age - classes where the corresponding sub - totals are $n_{21\ell}$ and $n_{22\ell}$.

Also within each age - class a time accumulator (mod a) is required, ξ_ℓ for males and ζ_ℓ for females, both of which are initialised to zero. Also, ξ_ℓ is reset to zero as soon as $\xi_\ell > a$, and similarly for ζ_ℓ. The details of the ADJ transfer procedure are then as below, where $y \equiv n_1$, $\tau \equiv \xi$ for the male age classes, and $y \equiv n_2$, $\tau \equiv \zeta$ for the female age - classes.

$$\delta y_\ell = \text{Min}\left\{\left[\frac{\eta y_{2\ell}}{a - \tau_\ell}\right], y_{2\ell}\right\} \quad \text{for } \tau_\ell < a,^{(*)}$$

$$= y_{2\ell} + \left[\frac{y_{1\ell}(\tau_\ell - a)}{a}\right] \quad \text{for } \tau_\ell \geq a.$$

Then for $\tau_\ell < a$,

$$y_{2\ell} \longrightarrow y_{2\ell} - \delta y_\ell$$

$$y_{1\ell} \longrightarrow y_{1\ell} + \delta y_{\ell-1}$$

and for $\tau_\ell \geq a$,

$$y_{2\ell} \longrightarrow y_{1\ell} + \delta y_{\ell-1} - \left[\frac{y_{1\ell}(\tau_\ell - a)}{a}\right]$$

$$y_{1\ell} \longrightarrow 0$$

and $$\tau_\ell \longrightarrow 0.$$

(*) Here $[x]$ means the integral part of x, in the usual way.

The M/F decision procedure determines the sex of the selected group according to the scheme that it is male if

$$0 \leq u < \frac{n_m}{n_m + n_f}$$

and female otherwise, where u is a realisation of the random variable U, uniformly distributed on [0,1] and where

$$n_m = \sum_{\ell=1}^{C} n_{1\ell} \text{ and } n_f = \sum_{\ell=1}^{C} n_{2\ell}$$

and so $j = n_m + n_f$.

The general principles governing choice of an appropriate function $\theta_1(x)$ for the age component of the birth function have been described in sub - section 6.4.4. A simple ramp function would probably suffice. However, taking into account GRUBB'S data for the survival pattern of lambs born to ewes by age, and also weight of dams, JEWELL et al.(1974) Chapter 5, Fig. 10.5, and by summing over weights, it is possible to specify $\theta_1(x)$ in greater detail. Using this data it was found that $\theta_1(x)$ takes the form

$$\theta_1(x) = 0 \quad \text{for} \quad 0 \leq x < x_1,$$

$$\theta_1(x) = y_1 + \frac{(y_2 - y_1)(x - x_1)}{x_2 - x_1} \quad \text{for} \quad x_1 \leq x < x_2,$$

$$\theta_1(x) = y_2 + \frac{(y_3 - y_2)(x - x_2)}{x_3 - x_2} \quad \text{for} \quad x_2 \leq x < x_3$$

and $\theta_1(x) = y_3 \quad \text{for} \quad x \geq x_3,$

where $x_1 = 10$, $x_2 = 24$, $x_3 = 36$, $y_1 = .28$, $y_2 = .735$ and $y_3 = 1.0$.

The function $\phi_1(t)$ has been defined fully in the main text and there is nothing further to add here. Also the construction of the age components $\theta_{21}(x)$ and $\theta_{22}(x)$ respectively, of the male and

female death rates on the basis of equation 6.4.5(1) and GRUBB'S mortality data by age, JEWELL et al.(1974) Chapter 10, Table 10.13, presents no special problems. For either sex, if Y_i is the total number of individuals at the beginning of year $i + 1$ $(i = 0,1,2,\ldots,10)$; then in order to smooth out the irregularities in the data, a polynomial

$$d_k(x) = c_0 + c_1 x + \ldots + c_k x^k$$

is fitted to the transformed dats $\ell n(Y_i)$. This can readily be effected by NAG routine E02ACF. By trial a suitable value k was found to be 5. As the survivorship function L(x) and the fitted polynomial $d_k(x)$ are related by

$$L(x) = \exp\left[d_k(x)\right]$$

then equation 6.4.5(1) now takes the form

$$\theta(x) = -d_k'(x) = -\sum_{i=1}^{k} i c_{i-1} x^{i-1}$$

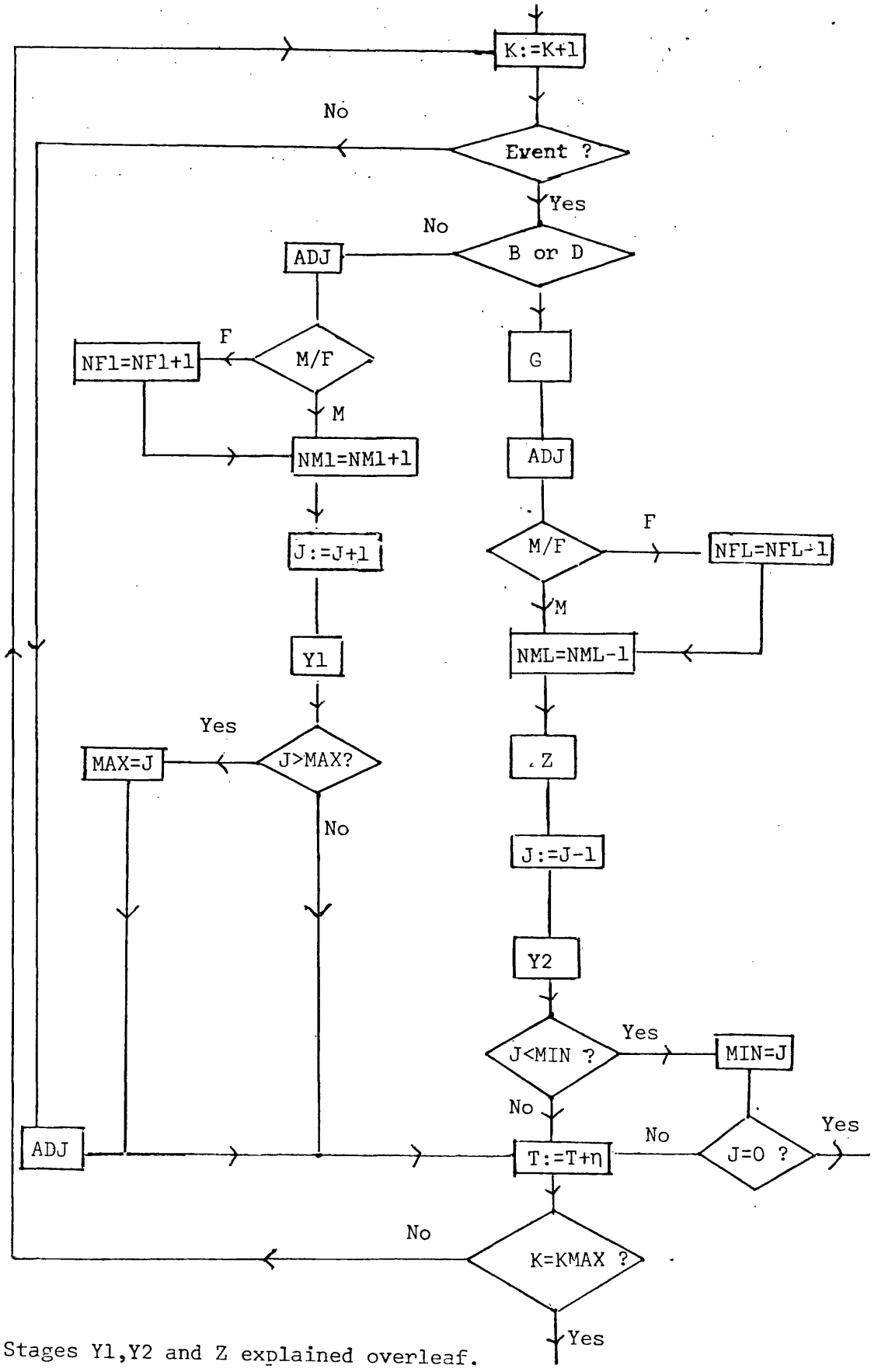
Note that the nature of the time component $\phi_2(t)$ of the death functions, by which, in accordance with equation 6.4.5(2), $\phi_2(t) = 0$ unless $0 \leq t \leq 3$, implies a rescaling of x to x/4. Thus θ_{21} is evaluated as $\theta_{21}(x/4)$ and θ_{22} as $\theta_{22}(x/4)$.

It only remains to comment on the numerical values adopted for a, η and C, and also on the computer time involved. As described in the main text, the A1 age specification requires C = 120 with a = 1. With this assignment the value η = .1 (i.e. a/10) was found to be satisfactory. However, with a total, therefore, of 240 age classes the simulation inevitably makes very heavy demands on computer time. In fact, it turns out that only about 60 time increments η, or about 12 actual jumps, on average, can be effected in 1 second of CP time on the SWURCC 2980 machine.

In the case of the A2 age specification where now there are only 4 age classes altogether, defined by $0 \leq x < 12$ and $12 \leq x \leq 120$, both for males and females, it was found that about 800 time increments, or equivalently about 160 actual jumps on average, could be effected in 1 second of 2980 CP time.

FIG. A4.1

SCHEME OF RUN LOOP FOR SIMULATION OF SHEEP POPULATIONS OF ST. KILDA



Stages Y1,Y2 and Z explained overleaf.

COMMENTS ON FIG. A4.1

(1) At Y1 death rate is scaled up if $j > N_c$, in accordance with the scheme described in Section 6.6. Similarly, at Y2, if j falls below N_c then the death rate is scaled down in accordance with the scheme.

(2) At Z birth function is set to zero at appropriate instant if either total number of males or females is equal to 0.

APPENDIX 5

THE NUMERICAL INVERSION OF LAPLACE TRANSFORMS BY THE METHOD OF BELLMAN, KALABA AND LOCKETT.

A5.1 GENERAL DESCRIPTION OF THE METHOD

The basic problem is to determine the function f(t) numerically when for a known function h(.),

$$\int_0^\infty e^{-st} f(t)dt = h(s), \quad (s > 0). \tag{1}$$

First put $e^{-t} = x$ to obtain

$$\int_0^1 x^{s-1} g(x)dx = h(s) \tag{2}$$

where $g(x) \equiv f(-\ell nx)$. Now integrals such as (2) can be calculated to a high degree of accuracy by standard quadrature formulae based on some suitable system of orthogonal polynomials on $[0,1]$. One such system is the shifted LEGENDRE polynomials $P_M^*(x)$ which are related to the usual LEGENDRE polynomials, $P_M(x)$, by

$$P_M^*(x) = P_M(2x - 1).$$

If therefore, $x_1, x_2, \ldots, x_M$ are the M zeros of $P_M^*(x)$ and $w_1, w_2, \ldots, w_M$ the corresponding GAUSS quadrature weights then from (2),

$$\sum_{j=1}^{M} w_j x_j^{s-1} g(x_j) \simeq h(s) \tag{3}$$

Taking therefore M suitable values of s, $s_1, s_2, \ldots, s_M$, say, we have the system of linear equations

$$\sum_{j=1}^{M} w_j x_j^{s_i-1} g(x_i) = h(s_i) \quad (i = 1, \ldots, M) \tag{4}$$

Writing these as

$$\underline{Q}_M \underline{g} = \underline{h} \tag{5}$$

therefore, where $\underline{Q}_M$ is the M × M matrix $\left\{ w_j x_j^{s_i - 1} \right\}$, (i = 1,...,M and j = 1,...,M), $\underline{g}' = \left(g(x_1) \ldots . g(x_M) \right)$ and $\underline{h}' = \left(h(s_1) \ldots . h(s_m) \right)$ we have the formal solution

$$\underline{g} = \underline{Q}_M^{-1} \underline{h} \tag{6}$$

for the values of f at $t_i = - \ell n(x_i)$, i = 1,...,M.

Theoretically the s_i can be any distinct values of s, but BELLMAN takes them simply as 1,2,...,M. Different sets of s_i have been tried here but these have not led to any improvement in the accuracy of the results.

A5.2 EXTENSION OF THE TIME SCALE

From equation A5.1(1) it follows that, for any k > 0,

$$k \int_0^\infty e^{-st} f(kt) dt = g(s/k) \tag{1}$$

Thus

$$f(kt) = L^{-1}\{k^{-1} g(s/k)\} \tag{2}$$

where for any function of s, h(s), $L^{-1}\{h(s)\}$ will denote its inverse LAPLACE transform. In this way, by suitable choice of k, the time scale can be extended to include any pre - assigned value of t. That such an extension is necessary is clear from the fact that even for a relatively large value of M, e.g. M = 15, the largest value of the t_i is only about 5.12.

It is also easy to show that

$$L^{-1}\left\{ k^{-1} g\left[\frac{s + a}{k} \right] \right\} = e^{-at} f(kt) \tag{3}$$

and then on the basis of (3) to evaluate the inverse of g(s) for a various values of a, as appropriate. This modification of the method

of BELLMAN et al. was found to be particularly effective for the inversion of such forms of g(s) as, for example, $\frac{m!}{s^{m+1}}$ and $\frac{\omega}{s^2 + \omega^2}$ to t^m and $\sin(\omega t)$, respectively, where otherwise poor results were obtained. However, it effected little, if any, improvement in the case of the negative exponential $e^{-\alpha t}$, $(\alpha > 0)$.

A5.3 EVALUATION OF THE ZEROS AND WEIGHTS FOR $P_M^*(x)$ AND OF THE ELEMENTS OF THE MATRIX $\underline{Q}_M^{-1}$

BELLMAN et al. give the values of the zeros and weights for the shifted LEGENDRE polynomial $P_M^*(x)$ and also the elements of $\underline{Q}_M^{-1}$ for $3 \leq M \leq 15$ to 15 significant figures. The method of obtaining these values originates from a technical memorandum by GAWLICK(1958) who obtains them for $P_M(x)$ for $2 \leq M \leq 64$ to 20 signicant figures. Once these numbers are available then it is a simple matter to obtain the elements of the matrix $\underline{Q}_M$ and hence of $\underline{Q}_M^{-1}$ by a standard matrix inversion procedure.

All the above were checked and $\underline{Q}_M$ was inverted to $\underline{Q}_M^{-1}$ using NAG routine F04AEF. The maximum relative error between the values of the elements of $\underline{Q}_M^{-1}$ obtained in this way and those given by BELLMAN et al. was found to be of the order of 10^{-6} for $8 \leq M \leq 15$. This seems surprisingly large especially as double precision was used throughout.

Consequently the moments of the distribution $\{p_{ij}(t)\}$ for a few cases of the SL process were evaluated using both sets of values of the elements of $\underline{Q}_M^{-1}$, in order that a comparison could be made. It was found that for the 4^{th} moments the maximum relative error for any value of t considered was of the order of 10^{-2}, though this was very

exceptional. For the lower order moments the maximum relative error was found to be 10^{-3} at most, for any value of t considered.

Actually the computing of $\underline{Q}_M^{-1}$ rather than the reading of it from a data file adds only about 5 to 10% to the overall computer time requirement for the evaluation of the moments of the distribution $\{p_{ij}(t)\}$ at several hundred values of t. (Such a large number of values of t can be considered in view of the time scale extension technique described in the previous section.) It is therefore quite possible to consider other values for s_j, e.g., $\frac{1}{2}, \frac{2}{2}, \ldots, \frac{M}{2}$ or $2,4,\ldots,2M$ to see if any improvement in accuracy can be obtained. However, it was found that to take $s_j = j$, or at least very nearly so, appeared to lead to optimal results in this respect.

APPENDIX 6

EVALUATION OF THE DISTRIBUTION OF STATES OF THE SL PROCESS AT VARIOUS VALUES OF t BY THE METHOD OF BELLMAN ET AL. APPLIED TO EQUATIONS 2.2(10).

Equation 2.2(10) can be written as

$$-\lambda_{j-1}\bar{P}_{i,j-1}(s) + (s + \lambda_j + \mu_j)\bar{P}_{ij}(s) - \mu_{j+1}\bar{P}_{i,j+1}(s) = \delta_{ij} \qquad (1)$$

where $j = 0,1,2,\ldots,N$ and $\bar{P}_{i,-1}(s) = \bar{P}_{i,N+1}(s) = 0$. Now for any $s > 0$ this tridiagonal system of equations can readily be solved by a standard elimination procedure for the N + 1 quantities $\bar{P}_{ij}(s)$. Thus following the methodology and notation in Appendix 5 the values of $P_{ij}(t)$ at times t_ℓ, ($\ell = 1,\ldots,M$) can be computed from

$$P_{ij}(t_\ell) = \sum_{s=1}^{M} R_M^{(\ell s)} \bar{P}_{ij}(s) \qquad (2)$$

where $R_M^{(\ell s)}$ is the ℓs^{th} element of the matrix Q_M^{-1}.

Now, as pointed out earlier, since e.g., t_M is only about 5.12 for M = 15 and cannot be significantly increased by choosing a suitably large, but numerically realistic, value of M, the need to rescale t is obvious when one considers the magnitude of the mean extinction times, τ_i, for the various cases of the SL process considered so far. Thus using equation A5.2(2), equation (2) above is now replaced by its more general form

$$P_{ij}(kt_\ell) = k^{-1} \sum_{s=1}^{M} R_M^{(\ell s)} \bar{P}_{ij}(s/k) \qquad (3)$$

as the basic formula of computation. Moments of any order, ν, can then be obtained at the same values of t from

$$m_{i\nu}(kt_\ell) = \sum_{j=1}^{M} j^{\nu} p_{ij}(kt_\ell) \qquad (4)$$

and likewise, values of $G_i(z,t)$ for any value of z of interest from

$$G_i(kt_\ell,z) = \sum_{j=0}^{M} z^j p_{ij}(kt_\ell) \qquad (5)$$

The choice of k is governed fundamentally by the magnitude of τ_i. Also there is the factor that that for any $M \geq 3$ the values, t_ℓ, of t are not uniformly distributed over the interval $[0,t_M]$, but become increasingly less dense towards the right - hand end. This effect is exhibited in Table A6.1 which shows, in order, all 92 values of t_ℓ for $\ell = 1....,M$ and $M = 8,9,...,15$.

The problem of choosing a range of suitable values of M is largely a matter of experiment and compromise. On the one hand, if M is too small then the results cannot attain a satisfactory degree of accuracy. On the other, if M is too large, then $\underline{Q}_M$ becomes unstable and in consequence spurious oscillations will become evident in the moments of the distribution of states regarded as functions of time. In fact, it was found that the NAG routine F04AEF failed, on account of overflow problems, to invert the matrix $\underline{Q}_M$ for M in exces of 22. Nevertheless, it was found that the output was completely stable for $8 \leq M \leq 15$ and since further there was very close agreement between the solutions obtained for these 8 values of M, it was decided to use them all. This decision also helped to prevent too sparse a distribution of values of moments with respect to t when the time-scale was extended to very large values of t. Some actual cases of the SL process will now be discussed.

For SL(.12, .1, 10, 100), for example, where the mean time to extinction for an initial state i = 10, τ_{10}, is 3.70×10^2 (See Table 2.3), it is appropriate to take k = 1,10 and 100 together with M = 8,9,...,15. Such a choice of values of k and M monitors the process at $3 \times 92 = 276$ values of t, the largest of which is 512, and also provides an adequate density of such instants of evaluation towards the right - hand end of the interval of t, $[0,512]$. Similarly, for SL(.15, .1, 10, 100) where $\tau_{10} = 2.28 \times 10^4$, suitable values of k were found to be 1, 10^2 and 10^4 which together with $8 \leq M \leq 15$ takes M up to 5.12×10^4.

On the other hand, for SL(.2, .1, i, 100) where τ_i ($i \geq 10$) is of the order of 10^9 it does not appear to be possible to obtain reliable values of $m_{i\nu}(t)$ for $k > 10^6$, so restricting t, in view of the limitation on M described above, to a maximum of 5.12×10^6. For k in excess of this value spurious oscillations were found to persist in the calculated moments over the range of t considered. This is essentially a numerical stability problem due to the smallness of s/k. Of course, this does not prove to be a serious limitation generally, for the large t solution described in Section 3.6 is available to complete the picture where necessary.

The computer time requirements are slight, especially when compared with those for the numerical integration method described in Section 3.3 and Appendix 8. Thus for any one case where N = 100 it is possible to calculate the entire distribution $\{p_{ij}(t)\}_{j=0}^{N}$ and also $\mu_i(t)$, $\sigma_i(t)$, $\eta_i(t)$ and $\kappa_i(t)$ for 276 values of t in about 30 seconds of CP time on the SWURCC 2980 computer. Actually about half this time is used to reorder the results obtained with respect to t,

this being necessary in view of the fact that the zeros of $P_n^{(*)}$ interlace those of $P_{n+i}^{(*)}$ for all $n > 1$. Again it should be pointed out that, in any case, the total CP time requirement does not depend on t and it is this fact which makes the method particularly valuable.

TABLE A6.1

THE NEGATIVES OF THE LOGARITHMS (BASE e) OF THE ROOTS OF THE SHIFTED LEGENDRE POLYNOMIAL $P_M^*(x)$, FOR M = 8, 9, ..., 15, ARRANGED IN ASCENDING ORDER OF MAGNITUDE.

0.006	0.007	0.008	0.009	0.011	0.013	0.016
0.020	0.032	0.036	0.042	0.049	0.058	0.070
0.079	0.086	0.090	0.104	0.107	0.122	0.145
0.148	0.170	0.175	0.197	0.215	0.231	0.241
0.271	0.275	0.278	0.323	0.333	0.361	0.380
0.412	0.416	0.454	0.486	0.510	0.525	0.554
0.575	0.591	0.693	0.693	0.693	0.693	0.807
0.827	0.854	0.896	0.918	0.955	1.007	1.078
1.085	1.152	1.194	1.261	1.288	1.417	1.425
1.439	1.539	1.578	1.643	1.721	1.831	1.856
1.982	2.003	2.162	2.286	2.311	2.449	2.501
2.578	2.696	2.874	3.038	3.189	3.330	3.462
3.919	4.140	4.339	4.520	4.686	4.840	4.982
5.115						

APPENDIX 7

NUMERICAL SOLUTION OF EQUATION 5.5(12)

Taking LAPLACE transforms of equation 5.5(12) yields

$$\bar{b}(s) = \bar{R}(s) - N^{-1}L\left\{y(t)R(t)\right\} \tag{1}$$

where, as previously, for any function of t, f(t), $\bar{f}(s)$ or $L\left\{f(t)\right\}$ will denote its LAPLPACE transform to the s - domain, and where

$$R(t) = g(t) + \int_0^t \ell(y)b(t - y)\,dy. \tag{2}$$

Thus as $$\bar{R}(s) = \bar{g}(s) + \bar{\ell}(s)\bar{b}(s), \tag{3}$$

then it follows from equations (1) and (3) above and also equation 5.5(6) in the main text that the value of $\bar{b}(s)$ for a prescribed value of s can be calculated by the iterative scheme,

$$\bar{R}_j(s) = \bar{g}(s) + \bar{\ell}(s)\bar{b}_j(s) \tag{4}$$

$$\bar{y}_j(s) = \frac{\bar{b}_j(s) + y(0)}{s + \mu} \tag{5}$$

and $$\bar{b}_{j+1}(s) = \bar{R}_j(s) - N^{-1}L\left\{y_j(t)R_j(t)\right\} \tag{6}$$

subject to a suitable initial value, $\bar{b}_0(s)$ say, for $\bar{b}(s)$.

For the type of birth function considered here, namely

$$\lambda(x) = \frac{b\beta}{\Gamma(q)}(\beta x)^{q-1}e^{-\beta x} \quad (\beta > 0,\ q > 1) \tag{7}$$

$\bar{\ell}(s)$ takes the simple form

$$\frac{b\beta^q}{(s + \beta + \mu)^q}, \tag{8}$$

or with $q = 2$, the value of q actually used in the cases considered,

$$\bar{\ell}(s) = \frac{b\beta^2}{(s + \beta + \mu)^2} \tag{9}$$

Also for the initial age distribution

$$A_0(x) = y(0)\alpha^2 x e^{-\alpha x} \tag{10}$$

$$\bar{g}(s) = \frac{y(0)b(\alpha\beta)^2}{(\alpha+\beta)^3} \cdot \frac{2(s+\mu+\beta)+\alpha+\beta}{(s+\mu+\beta)^2} \tag{11}$$

The functions $\bar{\ell}(s)$ and $\bar{g}(s)$ do not, of course, present any special computational problems so long as $s > 0$, as will always be the case here.

Note that the procedure requires at each iteration the transforming of $\bar{y}(s)$ and $\bar{R}(s)$ to $y(t)$ and $R(t)$, and then the transforming of the product $y(t)R(t)$ back to the s - domain. The transformation from the s to the t - domain is effected by the numerical inversion procedure of BELLMAN et al., as described in Appendix 5, and the transforming back to the s - domain is effected on the basis of equation A5.1(3). Such transformations can be carried out on the SWURCC 2980 computer in a matter of milliseconds, and thus provided the number of iterations is not too large, as generally was the case here, they do not in themselves give rise to excessive computer demands.

To some extent, of course, the number of iterations necessary to achieve convergence will be determined by the choice of $b_0(s)$. The obvious choice is

$$\bar{b}_0(s) = \frac{\bar{g}(s)}{1 - \bar{\ell}(s)} \tag{12}$$

i.e. the transform of b(t) for the unrestricted ($N = \infty$) process, and, in fact, this was found to be completely satisfactory for most cases. The iteration stops when for a prescribed ε

$$\left| \frac{\bar{b}_{j+1}(s) - \bar{b}_j(s)}{\bar{b}_j(s)} \right| < \varepsilon \qquad (13)$$

for all values of s that will be required for the inversion procedure, i.e. for $1 \leqslant s \leqslant M$. (Again, in view of the remarks in A5.3 we use these integer values of s, though as pointed out there other sets of values are theoretically possible.)

Having then acheived convergence for the $\bar{b}_j(s)$ and hence for the $\bar{y}_j(s)$ for all the M values of s it only remains to apply the inversion procedure to obtain the solution, y(t), at the M values of t namely, $t_1,\ldots,t_M$ defined in A5.1. The number of such values can be substantially increased by taking several values of M in the way described in Appendix 6. Here again, it was found that the 8 y(t) profiles obtained for M = 8,9,...,15 were in excellent agreement, so that in this way y(t) could be reliably evaluated for 92 values of t for $0 < t \leqslant 5.12$.

Nevertheless, in view of the actual time that y(t) takes to reach its steady state value, in general, the need to extend the time scale is obvious. Choosing values of k as appropriate therefore, the formula A5.2(2) was employed again to effect this. There are, however, no apparent theoretical criteria for choosing such values of k. They can only be determined empirically for each individual case.

No special computational problems were found in applying this technique here, provided k was not taken in excess of a critical value, k_L, say, which varies from case to case. For k in excess of k_L, even if convergence for all the $\bar{b}_j(s)$ could be achieved, y(t) was found to exhibit the spurious oscillation effect referred to in Appendix 6.

Fortunately however, it is not necessary, in general, to take k anywhere near k_L in order to obtain the entire y(t) profile up to its steady - state level.

With regard to computer time requirements, it should be mentioned that although the number of iterations required for the convergence of $\bar{b}_j(s)$ for all s increases rapidly with k, and in some cases hundreds of iterations proved to be necessary in order to obtain convergence, nevertheless the amount of computer CP time required was comparatively small. In fact, the evaluation and ordering of 276 values of y(t) arising from 3 values of k and M = 8,9,...,15 could be carried out on the SWURCC 2980 computer in about 5 seconds of CP time, for most cases.

It should be recorded, however, that there were a few cases of interest where the iteration scheme for the $\bar{b}_j(s)$ did fail to converge. These usually arose when β was near to, or actually equal to the critical value, β_c, defined in Section 5.5, or when b was relatively large. In this latter situation $y(\infty)$ is certainly greater than y(0), and y(t) increases rapidly towards this limiting value. It is this type of function which can sometimes prove a difficulty to the BELLMAN inversion procedure.

This might be resolved, however, by transforming s to s + a, where a is a suitable positive quantity, and then using the formula A5.2(3) to obtain $e^{-at}y(t)$. This artifice, as remarked in Appendix 5 works well for polynomials and might therefore deal satisfactorily with the numerical instability problem here. However, in view of the large number of cases for which results were obtained, it was not thought necessary to investigate this further.

Finally, no difficulties were found to arise for larger values of N (>100). If anything, increasing N led to a more stable iteration procedure. Thus it became clear that a technique had been developed by which a very wide range of cases of the deterministic logistic process with an age structure could be evaluated quickly and accurately.

APPENDIX 8

NUMERICAL INTEGRATION OF EQUATION 2.1(9) OVER D

The region of integration, D, and also the boundary conditions for the partial differential equation under consideration are defined in Section 3.3. For simplicity write this equation as

$$a(z)\frac{\partial G}{\partial z} + b(z)\frac{\partial^2 G}{\partial z^2} = \frac{\partial G}{\partial t} \qquad (1)$$

where therefore $a(z) = (1 - z)(\mu - \lambda_1 z)$, $\lambda_1 = \lambda(1 - \frac{1}{N})$, $b(z) = \lambda_2 z^2(1 - z)$ and $\lambda_2 = \frac{\lambda}{N}$.

Also let $z_i = (i - 1)h$ and $t_j = (j - 1)k$, where $1 \leqslant i \leqslant I$ and $1 \leqslant j \leqslant J$. The basic rectangle of the integration grid therefore has dimensions $h \times k$, and also, $Ih = 1$ and $Jk = T_{MAX}$, the final value of t up to which the process is taken.

Further, define $a_i \equiv a(z_i)$, $b_i \equiv b(z_i)$ and $g_{i,j} \equiv G(z_i,t_j)$. Then in accordance with the CRANK - NICHOLSON implicit method set up a finite - difference equivalent of (1) as follows.

$$\frac{a_i}{2}\left[\frac{g_{i+1,j} - g_{i-1,j}}{2h} + \frac{g_{i+1,j+1} - g_{i-1,j+1}}{2h}\right]$$

$$+ \frac{b_i}{2}\left[\frac{g_{i+1,j} - 2g_{ij} + g_{i-1,j}}{h^2} + \frac{g_{i+1,j+1} - 2g_{i,j+1} + g_{i-1,j+1}}{h^2}\right]$$

$$= \frac{g_{i,j+1} - g_{ij}}{k} \qquad (2)$$

for which the boundary conditions, as stated in Section 3.3, are now written in the form

$$g_{i1} = z_i^{n_0} \quad (n_0 = \text{initial population level}), \qquad (3)$$

$$g_{1j} = H\left[(j - 1)k\right], \qquad (4)$$

$$g_{I,j} = 1, \qquad (5)$$

where H(.) is defined by equation 3.3(2).

Equation (2) can be rearranged to the form

$$A_i g_{i+1,j+1} + B_i g_{i,j+1} + C_i g_{i-1,j+1} = D_{ij} \tag{6}$$

where

$$A_i = \frac{a_i}{4h} + \frac{b_i}{2h^2}, \tag{7}$$

$$B_i = -\frac{b_i}{h^2} - \frac{1}{k}, \tag{8}$$

$$C_i = -\frac{a_i}{4h} + \frac{b_i}{2h^2}, \tag{9}$$

and

$$D_{ij} = -\left[\frac{a_i}{4h} + \frac{b_i}{2h^2}\right] g_{i+1,j} + \left[\frac{b_i}{h^2} - \frac{1}{k}\right] g_{ij} + \left[\frac{a}{4h} - \frac{b}{2h^2}\right] g_{i-1,j}. \tag{10}$$

Now equation (6) can be solved effeciently by, for example, the GAUSS — SEIDEL iteration procedure. To apply this method, equation (6) is written as

$$v_i^{(\ell+1)} = P_i v_{i+1}^{(\ell)} + Q_i v_{i-1}^{(\ell+1)} + R_{ij} \tag{11}$$

where $v_i^{(\ell)}$ is the ℓ^{th} iterate of $v_i \equiv g_{i,j+1}$, $(\ell = 0,1,2,\ldots)$, $P_i = -A_i/B_i$, $Q_i = -C_i/B_i$ and $R_{ij} = D_{ij}/B_i$. The scheme is started by putting $v_i^{(0)} = g_{ij}$ and, in the usual way, iteration on ℓ ceases when for all i,

$$\left| \left\{ v_i^{(\ell+1)} - v_i^{(\ell)} \right\} / v_i^{(\ell)} \right| < \varepsilon$$

where ε is a preassigned small positive quantity.

The amount of computer CP time required to carry out the integration of equation (1), even to only relatively small values of t, is considerable. Thus, for example, with h = .005, k = .01 and

$\varepsilon = 10^{-12}$ it requires about 50 seconds of CP time on the CDC 7600 computer at ULCC to obtain $G(z,t)$ as far as $t = 100$ for any one of the cases $SL(\lambda, .1, 10, 100)$ where $\lambda = .12, .15$ or $.20$. The small value of h was found to be necessary in view of the fact that in the early developement of the process in time, $\frac{\partial G}{\partial z}$ can become large as $z \longrightarrow 1-$. Also, larger values of k would lead to perceptible accumulation of error with increasing t.

Of course, the CP time requirement could be reduced substantially by increasing ε by an order of magnitude, but trial runs indicated that this would lead to inaccuracy in some cases, and that it was necessary to adopt the very small value of 10^{-12} for ε as an overall safeguard even though there might be some cases where such a value is unnecessarily small. As, in fact, only a few cases needed to be considered, and these mainly for the purpose of verifying the results for $G(z,t)$ obtained by the LAPLACE Transform methodology described in Appendices 5 and 6, it was not thought worthwhile to investigate this matter further.

APPENDIX 9

NUMERICAL DERIVATION OF THE DISTRIBUTION $\{Q_j\}_{j=1}^{N}$ OF SECTION 2.7

The system of equations 2.7(8),(9) and (10) are equivalent to

$$Q_2 = \mu_2^{-1}(\lambda_1 + \mu_1 - \mu_1\xi)\xi \tag{1}$$

$$Q_3 = \mu_3^{-1}\left\{(\lambda_2 + \mu_2 - \mu_1\xi)Q_2 - \lambda_1\xi\right\} \tag{2}$$

and

$$Q_j = \mu_j^{-1}\left\{(\lambda_{j-1} + \mu_{j-1} - \mu_1\xi)Q_{j-1} - \lambda_{j-2}Q_{j-2}\right\} \tag{3}$$

for $j = 4,\ldots,N$, and

$$\xi + Q_2 + Q_3 + \ldots + Q_N - 1 = 0 \tag{4}$$

where $\xi \equiv Q_1$. For the basic SL model we also have that

$$\lambda_j = \lambda j(1 - \frac{j}{N}) \text{ and } \mu_j = \mu j$$

$j = 1,2,\ldots,N$.

Clearly therefore, Q_j $(j = 1,2,\ldots,N)$ is expressible as a polynomial of degree j in ξ, and thus equation (4) is a polynomial equation of degree N in ξ, which we write as

$$P_N(\xi) = 0 \tag{5}$$

Equation (5) can thus be solved in the usual way by the NEWTON - RAPHSON iterative scheme

$$\xi_{i+1} = \xi_i - \frac{P_N(\xi_i)}{P_N'(\xi_i)} \tag{6}$$

$i = 0,1,2,\ldots$ for which a suitable starting value was found to be $\xi_0 = 1/N$.

Note that

$$P_N'(\xi) = 1 + Q_2'(\xi) + \ldots + Q_N'(\xi) \tag{7}$$

where
$$Q_2'(\xi) = \mu_2^{-1}(\lambda_1 + \mu_1 - 2\mu_1\xi) \tag{8}$$

$$Q_3'(\xi) = \mu_3^{-1}\left\{(\lambda_2 + \mu_2 - \mu_1\xi)Q_2'(\xi) - \mu_1 Q_2(\xi) - \lambda_1\right\} \tag{9}$$

and
$$Q_j'(\xi) = \mu_j^{-1}\left\{(\lambda_{j-1} + \mu_{j-1} - \mu_1\xi)Q_{j-1}'(\xi) - \mu_1 Q_{j-1}(\xi) - \lambda_{j-2}Q_{j-2}'(\xi)\right\} \tag{10}$$

for $j = 4,\ldots,N$. Thus the derivatives $Q_j'(\xi)$ for $j = 2,\ldots,N$ can easily be evaluated and thus so can $P_N'(\xi)$. Also in the usual way iteration on i ceases when

$$\left|\frac{\xi_{i+1} - \xi_i}{\xi_i}\right| < \varepsilon$$

where ε is a preassigned small positive quantity. Here ε was set to 10^{-7}, and it was found that about 10 ETUS of CP time on the System 4 machine at Bath were required for each case.

Once, of course, the Q_j had been calculated, it was then a routine matter to compute, for example, the quantities $\mu^L(t)$ and $\sigma^L(t)$ defined by equations 3.6(3) and (4).

APPENDIX 10

NUMERICAL EVALUATION OF THE INTEGRAL 4.3(10)

To begin with write this integral as,

$$I = I_1 + I_2 \tag{1}$$

where

$$I_1 = \iint_{D_1} h(v,w)dvdw, \tag{2}$$

$$I_2 = \iint_{D_2} h(v,w)dvdw \tag{3}$$

and where D_1 is the region of the v - w plane defined by $0 \leqslant v \leqslant k$, $0 \leqslant w \leqslant k$ and $D_2 = D_0 - D_1$ where D_0 is the region defined by $0 \leqslant v \leqslant x$ and $0 \leqslant w \leqslant 1$, $(0 \leqslant k \leqslant x \leqslant 1)$. The initial aim is thus to determine the order of magnitude of I_1, in terms of k, as $k \longrightarrow 0$.

To this end therefore, note that within region D_1

$$h(v,w) = G_k \frac{1 - v}{(v + w)(a - b_1 v - b_1 w)} \left[\frac{a_1 - b_1 v - b_1 w}{a_1 - b_1 v}\right]^{\theta} e^{\phi w(1-v)} \tag{4}$$

where $G_k = 1 + O(k)$. Also, suppose further that $k = 1/N$ and $N \longrightarrow \infty$.

Then

$$\left[1 - \frac{b_1 v}{a_1}\right]^{\theta} = \left[1 - \frac{gv'}{N}\right]^{4N\rho}$$

$$= \left\{1 + O(k)\right\} e^{-g'v'} \tag{5}$$

where $v' = Nv$ ($\leqslant 1$ within D_1), $g' = 4g\rho$ and $g = 1/(\frac{1}{2} + \rho)$. Similarly,

$$\left[1 - \frac{b_1}{a_1}(v + w)\right]^{\theta} = \left\{1 + O(k)\right\} e^{-g'(v'+w')} \tag{6}$$

where $w' = Nw$. Also, as within D_1,

$$e^{\phi w(1-v)} = \left\{1 + O(k)\right\} e^{\phi w} \tag{7}$$

then (4),(5),(6) and (7) imply that

$$I_1 = H_k \iint_{D_1} \frac{1 - v}{(v + w)(a_1 - b_1 v - b_1 w)} e^{g'' w} dvdw \tag{8}$$

where $H_k = 1 + O(k)$, and where

$$g'' = \phi - g'N = 2N - 4g\rho N$$

$$= \frac{2N(\lambda - \mu)}{\lambda + \mu} = BN, \text{ say.} \tag{9}$$

Thus by the CAUCHY - SCHWARZ inequality for integrals,

$$I_1^2 \leqslant H_k I_3 I_4 \tag{10}$$

$$I_3 = \iint_{D_1} \frac{1 - v}{(v + w)(a_1 - b_1 v - b_1 w)} dvdw \tag{11}$$

$$I_4 = \iint_{D_1} e^{g'' w} dvdw \, . \tag{12}$$

Now it may easily be shown that

$$I_3 = \int_0^k \ell(v) dv \tag{13}$$

where $$\ell(v) = a_1(1 - v)\ell n \left[\frac{(k + v)(a_1 - b_1 v)}{v(a_1 - b_1 v - b_1 k)} \right].$$

Thus since $$\int_0^k (1 - v)\ell n(k + v) dv$$

$$= k\ell nk + (2\ell n2 - 1)k + O(k^2 \ell nk), \tag{15}$$

$$\int_0^k (1 - v)\ell nv dv = k\ell nk - k + O(k^2 \ell nk), \tag{16}$$

and $$\int_0^k (1 - v)\ell n \left[\frac{a_1 - b_1 v}{a_1 - b_1 v - b_1 k} \right] dv$$

$$= \int_0^k (1 - v) \left[\frac{b_1 k}{a_1} + O(k^2) \right] dv = O(k^2), \tag{17}$$

then $$I_3 = a_1^{-1} \left\{ (2\ell n2)k + O(k^2 \ell nk) \right\} = C + O(k^2 \ell nk) \tag{18}$$

where $C = 4\ell n2/(\lambda + \mu)$.

Also $$I_4 = k^2 B^{-1}(e^B - 1). \qquad (19)$$

Thus from (10), (18) and (19)

$$I_1 \leq Gk + O(k^2 \ell nk) \qquad (20)$$

where $$G = \sqrt{CB^{-1}(e^B - 1)}.$$

There are no singularities in $h(v,w)$ over D_2, and thus the numerical evaluation of I_2 presents no special problems. In this case it is based on the formula

$$\iint_S h(v,w)dvdw \simeq k^2 \sum_{i=1}^{9} q_i h(v_i,w_i) \qquad (21)$$

where the weights q_i are assigned in the basic square, S, in the manner described below, ABRAMOWITZ and SEGUN (1968), Chapter 25.

$$\begin{array}{lccc} & P_7 & P_3 & P_6 \\ S & P_4 & P_1 & P_2 \\ & P_8 & P_5 & P_9 \end{array}$$

The points P_i have coordinates (v_i, w_i), and, in particular, P_1 is the centre of S relative to which P_2 and P_4 have coordinates $(\pm d, 0)$, where $d = k\sqrt{\frac{3}{10}}$, and P_3 and P_5 are $(0, \pm d)$. Also relative to P_1 the points P_6, P_7, P_8 and P_9 are defined by $(\pm d, \pm d)$. Further, $q_1 = \frac{16}{81}$, $q_2 = q_3 = q_4 = q_5 = \frac{10}{81}$ and $q_6 = q_7 = q_8 = q_9 = \frac{25}{324}$. The error in formula (21) is $O(k^6)$.

The value of I_1/I_2 was found to be of the order of 10^{-5} and thus for the accuracy required here the contribution of I_1 to I could be regarded as negligible.

It was found that with $k = .01$ and $x = .1$, thus dividing up R

into 10^3 squares, and hence D_2 into $10^3 - 1$ squares, about 2 seconds of CP time on the CDC 7600 computer at ULCC was required to evaluate one case. In order to confirm accuracy, however, the values .005, .0025 and even .00125 were used for k in some cases with corresponding increases in computer time requirements. This last factor is, of course, directly proportional to x, as defined in equation 4.3(10), but independent of λ, μ and N, the other basic parameters of the SL process. In fact, it was found, for example, that about 10 seconds of CP time on the CDC 7600 computer were required when x = .5 and k = .01. If, however, k was then reduced to .0025, the CP time requirement went up to about 40seconds, which is considerable. For most cases, however, an accuracy of 2% could be achieved with k = 0.01.

FINAL NOTE

Since the completion of this research, two relevant papers, YAMAMOTO (1961) and PICARD (1963) have come to the author's attention. In the first of these there is a proof of what is essentially Theorem 2.1, though by a different method. However, the particular value of the proof given in this thesis is that it includes a formal LAPLACE Transform solution of the process in equation 2.2(8) which was shown in Chapter 3 to be capable of numerical evaluation.

The paper by PICARD contains a formal solution of the partial differential equation which defines the PGF appertaining to the distribution of states for a certain class of nonlinear processes with quadratic rates of which the SL process is a special case. This takes the form of equations 2.2(1) in which the real coeffecients β_{ijk} have an integral representation based on HEUN's generalised hypergeometric functions. The α_j which, it will be recalled are the eigen values of the matrix of Lemma 2 of Section 2.2, are not, however, obtained explicitly in terms of the process parameters.

Thus, it is difficult to see how, in analytic terms, such a formula can be developed to provide a simple overall description of the SL process such as was achieved at the end of Chapter 4 of this thesis. Moreover, in contrast to the LAPLACE Transform method of Chapter 3, it would appear that its direct numerical evaluation would require very large amounts of computer time.

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